

SINKING FOOD SUPPLY:
DOES COMPOSITION, DIVERSITY, OR QUANTITY
OF FOOD SUPPLY INFLUENCE MACROINFAUNAL
COMMUNITIES?

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COMMUNITIES?**

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ABSTRACT

The role that food supply may play in determining patterns of biodiversity of shallow-water benthic macrofaunal communities is not well understood. This work tests the hypotheses that different types, diversity, and amount of phytodetrital material will attract different species and diversity of colonizing fauna. *In situ* experimental enrichment patches were created on the muddy seafloor at 20 m depth in a small cove in Bonne Bay, Newfoundland. Separate experiments tested the importance of different types and amounts of phytodetritus by gently syringing material onto otherwise undisturbed sediment. Push core samples were collected by divers 1 week and 5 weeks after enrichment and the experiments were repeated during the summer and the fall to test the importance of different seasons. Ambient fauna were also sampled with push cores at approximately two-week intervals through the summer and early fall. A strong seasonal signal was detected within the macrofaunal community with significant abundance increases during the study period, and there was also evidence of a strong recruitment event. Nonetheless, the composition of the phytodetrital food pulses tested had little effect on macrofaunal community diversity, structure and species composition at this site. Varying amounts of phytodetrital pulse showed reduced species diversity with increased enrichment, but this response was rapid and quickly disappeared, suggesting that food patches are rapidly utilized and short lived. The rapid utilization of phytodetrital patches may be characteristic of productive Newfoundland waters, and the absence of a specialized response to phytodetritus by Bonne Bay macrofaunal communities suggests they may be less food limited than many other benthic environments.

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STATEMENT OF CO-AUTHORSHIP

All manuscripts based on this thesis were coauthored with Paul V. R. Snelgrove, except for chapter 3, which was used in the manuscript, Quijon, Kelly & Snelgrove (2008). In all instances, I was the principal contributor to project design and proposal, implementation of the field research component, analysis of data, and manuscript preparation.

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INTRODUCTION AND OVERVIEW

Interest in regulation of benthic biodiversity has increased in recent years (Snelgrove et al., 2000; 2004), driven in part by the observation that species richness in deep-sea sediments may rival diversity of tropical rainforests (Grassle & Maciolek, 1992). It has been argued that shallow-water and deep-sea sediments may not differ in terms of diversity (Gray, 1994), and although this argument is not universally accepted (Gage 1996; Snelgrove and Smith, 2002) the debate raises the question of which factors contribute to and maintain the diversity in sedimentary habitats given their relatively homogenous landscape?

Maintenance of biodiversity in the deep-sea has generated considerable debate, and many theories have been put forth to explain the paradox of deep-sea sedimentary biodiversity (reviewed in Snelgrove & Smith, 2002). Indeed, the theoretical and experimental frameworks for studies on biodiversity are actually greater for deep-sea systems than for shallow-water communities. In coastal areas it is thought that habitat heterogeneity, seasonality, predation, productivity, historical effects and nearshore disturbances such as storms and prolonged winds, to mention a few, can contribute to biodiversity patterns (Snelgrove, 2001). Generally studies are lacking, however, as to what effect the composition and diversity of food supply have on the maintenance of sedimentary biodiversity.

Benthic organisms are important for many reasons; some species are themselves the target of lucrative fisheries (a significant amount of the protein consumed by humans comes from the sea) (Hixon et al., 2001), and other benthic organisms are key prey species for significant commercial species such as cod (*Gadus morhua*), redfish (*Sebastes* spp.), and flatfish (e.g. *Pleuronectidae*) (Snelgrove, 2001). Apart from the direct benefits of harvesting benthic organisms, sedimentary fauna also provide ecosystem services. An ecosystem service is a benefit that humans derive from natural processes that occur within an ecosystem (Daily et al., 1997). Ecosystem services associated with sedimentary fauna include nutrient cycling, sediment stabilization, filtration, gas and climate regulation, leisure and recreation, and regulation of pollutant dynamics (Daily et al., 1997; Snelgrove et al. 1997; Hixon et al., 2001; Levin et al., 2001; Beaumont et al., 2007).

It is believed that much of the food supply for subtidal benthic organisms is derived from the overlying water column (Josefson & Conley, 1997); at temperate latitudes a significant part of this material may originate from the spring phytoplankton bloom (Graf, 1992; Smith et al., 2001; Snelgrove et al., 2000 and references therein). Multiple studies have observed a marked pulse in labile organic matter shortly after the spring bloom both in shallow (e.g. Graf et al., 1982; Grebmeier & Barry, 1991; Bertuzzi et al., 1996; Parrish, 1998; Beaulieu, 2002) and deep-sea (e.g. Billett et al. 1983) areas. In some cases the sunken phytodetritus forms a green “carpet” along the bottom (Smetacek, 1984). Measurements of heat production, oxygen demand and temperature show a strong benthic response during and after a sinking bloom in Kiel Bight (Graf et al., 1982) but the

study did not include a biodiversity component. Except for pollution studies there are few species-level studies on macrofaunal response to food inputs.

Bonne Bay is a fjord located on the west coast of Newfoundland, Canada within the boundaries of Gros Morne National Park. Its outer region splits into two inner arms, the East Arm which is a relatively deep basin (230 m) and the South Arm, which is much shallower (80 m). A shallow (12 – 15 m) sill located at the mouth of the East Arm impedes circulation to the deep basin, however, the South Arm is relatively open to the Gulf of St. Lawrence. Bonne Bay is an area of regionally high biodiversity because it is an ecotone between temperate and subarctic assemblages (Hooper, 1975). There is a wide range of benthic substrates, from large boulder and vertical bedrock walls, kelp beds, cobble and sands to fine silts and clays. This study focuses on communities associated with medium to fine sand.

This work is divided into four chapters. Chapter 1 is an exploratory chapter that examines seasonal changes in ambient fauna and environmental conditions. Chapters 2 and 3 report on *in situ* experimental manipulations designed to investigate sinking food supply as a factor that may influence benthic community structure and biodiversity. The objectives of Chapter 2 are to determine the effect of the composition and diversity of sinking food supply; while Chapter 3 examines the importance of the quantity of food supply, to determine if these factors influence benthic community structure. Chapter 4 summarizes the general findings and conclusions from the first 3 chapters.

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CHAPTER 1

BENTHIC COMMUNITY TEMPORAL DYNAMICS WITHIN A SHALLOW-WATER SUB-ARCTIC SEDIMENTARY COMMUNITY

1.1 INTRODUCTION

Traditional views on regions of high biodiversity (i.e. species richness) such as tropical rain forests, and corals reefs, attribute the high diversity to high habitat complexity or heterogeneity (Grassle & Morse-Porteous, 1987; Archambault & Bourget, 1996; Snelgrove & Smith, 2002). Sedimentary communities, though seemingly homogeneous, are dynamic systems with respect to time and space, and can be quite heterogeneous on small spatial and temporal scales (Morrisey, et al., 1992; Thrush et al., 2001) and may be characterized by high diversity (Gray, 1997).

Seasonal changes within sedimentary benthic macrofauna communities have been widely documented from shallow-water habitats (Dollar et al., 1991; Trueblood et al., 1994; Kelaher & Levinton, 2003) to the deep-sea (Lampitt, 1985; Josefson, 1986; Graf, 1992). Despite commonalities in each study, results from one area and community may not apply to a similar community in a different location. In strongly seasonal environments such as the northwest Atlantic, seasonal changes in water temperature and changes in phytoplankton production associated with the spring bloom may be particularly important for subsequent benthic species recruitment and community dynamics. Recent work (Levin et al., 2001; Snelgrove, 2001) underscores the issue of marine biodiversity as an area where the role of environmental variability is not well

understood. In particular the key factors that regulate marine sedimentary diversity remain unresolved (Snelgrove et al., 1996).

Shallow-water ecosystems rely on input from terrestrial (Frouin, 2000) and intertidal ecosystems (Levin et al. 2001), endogenous production by benthic microalgae (Gould & Gallagher, 1990), and sinking phytodetritus (Grebmeier et al., 1988; Parrish, 1998; and Stead & Thompson, 2003). All of these inputs have the potential to create patch mosaics akin to those proposed as key microhabitats for deep-sea ecosystems (Grassle & Sanders, 1973). In shallow-water habitats the patchy distribution of benthic infaunal communities has long been recognized (McCall, 1977; Morrissey et al., 1992, and references therein). Indeed, faunal abundances and composition may vary on scales of metres. Small scale patchiness, however produced, further emphasize the importance of local larval and juvenile colonization as elements for setting pattern (Snelgrove et al., 2001).

In high latitudes, major factors that influence benthic community structure include sediment heterogeneity, presence of seagrass (Orth et al., 1984 and Heck et al., 1995) temperature and food supply, where food supply can have a direct positive influence on biomass (Grebmeier et al., 1989). From this research in the Bering and Chukchi Seas, it was hypothesized that at high latitudes in areas where sediments are homogeneous, food is limiting and is especially important in regulating faunal diversity and abundance (Grebmeier et al., 1989). In southern Newfoundland, sediment chlorophyll-a levels and sedimentary organic carbon are the most important predictors of infaunal abundance

(Ramey & Snelgrove, 2003). In another Newfoundland bay, Parrish (1998) found that planktonic lipids sink with very little alteration through the water column and can then become incorporated into the benthic food chain. This finding also has ramifications for the quality of food that reaches the benthos; lipids have a high energy value and are thus an important fuel in marine ecosystems (Parrish, 1998).

Food supply is not the only variable thought to influence biodiversity and abundance in shallow-water communities, and other studies have demonstrated the importance of bioturbation (Widdicombe et al., 2000), predation (Schneider, 1978; Quijon & Snelgrove, 2005) bottom currents (Snelgrove & Butman, 1994; Bradbury & Snelgrove 2001 and references therein), larval supply (Snelgrove et al., 1999) disturbance (Widdicombe & Austen, 2001), seasonality (Trueblood et al., 1994) and physical processes such as storms and prolonged winds (Norkko et al., 2002). In all likelihood all these factors, or some combinations thereof, work collectively (e.g. Widdicombe & Austen, 2001) to influence biodiversity patterns. This study focuses on food supply as a potential factor driving biodiversity pattern.

Arguably the important food-related event for sedimentary fauna in temperate waters is the spring phytoplankton bloom. Smetacek (1984) argues that sediments can receive the majority of annual organic matter input during the spring bloom. This sedimentation of organic matter has been shown to stimulate benthic metabolism (Graf et al., 1982), and in areas of intense sedimentation, sinking phytodetritus can be seen on the bottom as a

thick “carpet” that can be visible for several days (Smetacek, 1984; Lampitt, 1985). At temperate and sub-arctic latitudes such as in Newfoundland and Labrador, surface-water production peaks during the spring bloom (late April – May), declines dramatically during the summer months, increases again in the fall (late August – September), and then decreases to very low levels over the late fall and winter (September to March) (Tian et al., 2001). The bloom is made up chiefly of diatoms (~98%) where cell densities in surface waters peak at concentrations on the order of 10^5 cells L^{-1} (McKenzie, 1994).

The objectives of this chapter are to gain an understanding of benthic community dynamics with respect to the seasonal changes in organic flux. I hypothesize that changes in abundance, composition and diversity within the benthic community will occur after an important food pulse (such as the spring bloom) reaches the sediment. I also measure parameters to better understand the state of the food supply to the sediment. This chapter, by describing natural, seasonal variation in Bonne Bay subtidal sedimentary communities provides a framework for the subsequent experimental chapters.

1.2 MATERIALS AND METHODS

The majority of the fieldwork involved with this project was carried out by SCUBA divers. To carry out this research safely, a depth of 20 m (60 feet) was chosen. This depth provides a relatively stable bottom environment, not effected by waves, where working time is reasonable without necessitating decompression or special gas mixes.

1.2.1 Sampling Site

Bonne Bay is a fjord located on the west coast of Newfoundland, Canada within Gros Morne National Park. The bay consists of two deep basins, the East Arm (max. depth 230 m), which has restricted flow as a result of a 15-m sill located at the mouth of the basin; and the South Arm (max. depth 100 m), which has more open exchange with the Gulf of St. Lawrence (Hooper, 1975). “Small Cove” is located within South Arm (Figure 1.1). Several factors contributed to the selection of the study site. Although the site is located near several small coastal communities, the cove itself is uninhabited and is distant from any significant sources of anthropogenic inputs of organic matter. This site had the highest biodiversity of a handful of sites surveyed in Bonne Bay (Quijon 2001, pers. comm.). This site is also well sheltered, with relatively low boat traffic, which proved helpful in terms of logistics associated with sampling and maintaining the integrity of the experiments described in Chapters 2 and 3.

1.2.2 Field Sampling

Sediment cores were taken throughout the spring, summer, and fall of 2002 within ~5 m of a surface marker (49°28.872' N, 57°54.551' W) anchored in the cove. Four replicate cores (6.5 cm diameter, 20 cm length) were collected on each of nine sampling dates (total of 36 cores) by divers who pushed the cores into the sediment to ~10 cm depth. Cores were corked and transported upright to the laboratory where they were sectioned into 0-2 cm, 2-5 cm, and 5-10 cm strata, prior to washing with filtered seawater over a 300 µm sieve. Samples were placed in glass sample jars and fixed in 10% buffered formalin solution for at least 24 hours, before rinsing them with fresh water and transferring them to 70% alcohol with Rose Bengal stain. The upper two fractions (top 5 cm) of all samples were sorted and organisms were identified to the lowest possible taxonomic level, which was usually species. For the purposes of this study a juvenile was described as recognizable to family or genus but too small to be identified to species using a conventional light microscope (max. magnification 1000x).

Qualitative phytoplankton samples were taken using a Sea-Gear® ring net with 20 µm mesh and a 30 cm diameter mouth. The net was towed just below the surface for 1 minute; towing speed was variable to maintain minimum tension on the net. Samples were fixed using Lugol's Iodine, to give the 'weak-tea' colour, and then preserved in 2% buffered formalin solution. A 1 or 2 ml aliquot of each sample was placed in a well on a large slide, filtered seawater was added to fill the well. Slides were then observed under an inverted phase-contrast microscope and observations were recorded.

Water samples for chlorophyll and phaeopigment analysis were collected using a 2 L Niskin bottle. Samples were collected in duplicate at the surface and at 1 m above bottom. A 100-ml aliquot from each sample was filtered on a Whatman GF/F filter, the filter was then transferred to 10 ml of acetone and placed in the freezer, in the dark, until analysis in a TD Model 10 fluorometer.

Mini-cores (60 ml syringes with tip removed) were transported to the bottom by divers and pushed several centimetres into the sediment to sample sediment for CHN analysis. A single core was collected each for sediment CHN analysis, and sediment chlorophyll and phaeopigment analysis on each fauna sampling day. For sediment CHN analysis the top 1 cm was removed from each core, and frozen until analysis. Samples were then freeze-dried at -60°C and analyzed in duplicate (2 replications per sampling date) using a CHN Analyzer (Perkin-Elmer Model 2400) (Ramey & Snelgrove, 2003). Samples for sediment chlorophyll and phaeopigments were collected in the same manner. Sediment samples for pigment analysis were kept frozen in the dark until processing. Chlorophyll and phaeopigments were extracted using acetone and measured in a fluorometer as described above.

1.2.3 Data Analysis

Environmental variables (Sediment CHN and pigments, and water pigments) were compared using one-way ANOVA with date as factor. For cases where ANOVA assumptions were not met; data were log transformed. If assumptions were still not satisfied, p-values were obtained by a randomization test with one-way ANOVA;

calculated p-values were compared with p-values calculated by randomly generated F-values (500 iterations with replacement) to determine the reliability of the calculated p-value. Linear regression analysis was used to predict abundance (N) and benthic species richness (S) as a function of environmental variables. Examination of residuals revealed that assumptions of normality, heterogeneity and independence were met in all cases. In several cases sampling dates for fauna and for environmental data did not coincide; in those cases the incomplete sampling dates were omitted from analysis. Phytoplankton data were analyzed qualitatively and observations were recorded on numerically-dominant species and species richness.

Community composition was compared among sampling dates using CNESS (Chord-Normalized Expected Species Shared), which is discussed in Trueblood et al. (1994). CNESS is a dissimilarity index related to Orloci's (1978) chord distance and Grassle and Smith's (1976) NESS (Normalized Expected Species Shared). The CNESS index was chosen because of its ability to cope with both rare and abundant species (Grassle & Smith, 1976). The sample x species matrix was transformed to a normalized hypergeometric probability matrix (H); this probability matrix was used in a principal components analysis of hypergeometric probabilities (PCA-H). Since this matrix is a metric scaling, Gabriel biplots (Gabriel, 1971) can be overlaid to identify species that are important with respect to variation of CNESS and therefore drive community pattern (see Ramey & Snelgrove, 2003; Quijon & Snelgrove, 2005; and Trueblood et al., 1994 for further details). Preliminary analysis indicated that two samples (one from September

and one from October) had substantially lower abundances and species richness relative to all other samples and represented outliers; these two samples were omitted for the remainder of the analyses. Primer v.5 was used to cluster the samples based on Bray-Curtis similarity. Several combinations of data analysis with transformed and untransformed data were examined and produced similar patterns; the result presented here is untransformed data with complete linkages.

Univariate measures based on abundance (N), species richness (S), evenness (J), Shannon-Weiner Index (H'), Margalef's Index (D), and ES[30] (Expected species shared based on a random draw of 30 individuals) as well as rarefaction curves were generated using Primer v.5. Means and 95% confidence intervals were plotted and each measure was compared by one-way ANOVA with date as factor. Where residuals did not meet assumptions of ANOVA, the randomization technique described above was used. In the case of ES[30], samples that had low abundance (i.e. fewer than 30 individuals) were not included in the analysis (this occurred only for one of the September replicates). For rarefaction curves, means and 95% confidence intervals were calculated for multiples of 5 individuals.

1.3 RESULTS

1.3.1 Environmental Observations

Qualitative phytoplankton samples indicate that the overlying water column changed considerably during the sampling period with respect to community composition.

Samples taken in early June (June 6) were dominated by the diatoms *Detonula*

confervacea and *Bacterosira bathyomphala*; however, species richness was high at this time compared to subsequent sampling dates and included several species of *Chaetoceros* sp., *Thalassissira* sp. and *Protoperidinium* sp., *Skeletonema* sp., *Pseudo-nitzschia* sp., *Thalassionema nitzschioides*, *Dactyliosolen fragilissimus*, *Dinophysis* cf *acuminata*, *Dictyocha speculum*, *Navicula* sp. and *Leptocylindrus danicus*. Later in the same month (June 19) the dominant species were the Chrysophyte *Dinobryon belgacea* and *Dinobryon balticum* whereas the diatoms *Chaetoceros debilis*, and *Pseudo-nitzschia* sp. most likely contained most of the chlorophyll in the sample. Species richness in the plankton had decreased, and other common taxa included *Protoperidinium curtipes* (which is a smaller species than the *Protoperidinium* sp. seen in the June 6th samples) and *Dinophysis norvegica*. By late July (July 22) the phytoplankton was dominated by the diatom *Ceratium arcticum* and phytoplankton species richness was low compared to previous and subsequent sampling dates. Some tintinnids were present, and zooplankton and zooplankton faecal pellets were quite common. In late August (August 28), *Ceratium* sp. were again dominant, however, at this time *Ceratium fusus* was approximately 4 times more abundant than *Ceratium arcticum*. Some common organisms included several species of *Protoperidinium* sp., *Dinophysis norvegica* and zooplankton. Samples from mid-September (September 19) indicated a bloom of *Skeletonema costatum*, and the presence of *Navicula* sp. and *Thalassionema* sp.. By the end of the sampling period the phytoplankton was dominated by *Ceratium* spp. (*C. fusus* and *C. arcticum*). *Protoperidinium* sp. were present but was not abundant, and there

were very few zooplankton. Images of representative phytoplankton species are provided in Appendix A.

Water column measurements of chl-a and phaeopigments show high levels of pigment in the water column both at surface and at depth in May and then decreasing levels through July. Levels of pigment increased again in August and decreased to the lowest levels observed during the sampling period in October (Figure 1.2). A similar seasonal pattern was observed in the sedimentary organic carbon data described below. On May 21 the highest values for both chl-a and phaeopigments were in near-bottom samples, which may be indicative of a sinking food pulse and resuspension. It further highlights the patchy nature of food availability in time. Pigments were significantly different ($p < 0.05$) over the sampling period (Table 1.1) with the exception of surface chl-a ($F_{(7,8)} = 2.35$; $p = 0.127$). With a few exceptions (June 19, and August 28) there was no significant difference between surface and near-bottom pigment concentrations.

Analysis of sediment C and N levels shows that sediment carbon and nitrogen levels changed significantly over the sampling period (Table 1.1). Carbon and nitrogen levels were quite high in early spring (May 8th) and then decreased through to July 23rd. Carbon and nitrogen were higher on August 6th and then carbon decreased until October 14th; nitrogen levels remained consistently high during that period (Figure 1.3a). Sediment C/N ratios were relatively constant (ca 15) throughout the sampling period, however the lowest values were observed on July 23rd which coincided with the lowest values for

sedimentary carbon and nitrogen; and in the fall (September 21st and October 11th) when carbon levels dropped and nitrogen levels remained high (Figure 1.3b).

Sediment chl-a analysis revealed that chl-a input was quite variable in the early part of the year, but a pulse of phytoplankton biomass reached the sediment between May 8 and May 21 prior to stabilizing to a consistent, lower level towards late summer - fall (Figure 1.3c). Sediment phaeopigments were consistently higher (by an order of magnitude) than chl-a for the entire sampling period. Phaeopigments were also variable but were higher during the first half of the sampling period prior to decreasing to lower levels towards the late summer and fall (Figure 1.3c). Table 1.1 shows that changes between sampling date for sediment phaeopigments were significant whereas changes for chl-a were not.

1.3.2 Overview: Ambient Fauna

A total of 2649 individuals were collected from 36 cores for a total of 86 species of polychaetes, molluscs, crustaceans, nemerteans, echinoderms, hydrozoans, anthozoans and sipunculids. Many of the species were low in abundance and several only occurred once; only 2 taxa were present in every sample at each sampling date. The most abundant group by far were the polychaetes comprising 58 species and 53% of the total fauna. Bivalves and crustaceans/other comprised 33% and 14% of totals respectively. The fauna was highly uneven, in that the polychaetes *Paradoneis lyra*, *Prionospio steenstrupi*, *Pholoe tecta*; the bivalve *Astarte* sp., and the cumacean *Diastylis lucifere* made up 45% of the total fauna. The most abundant species (Figure 1.4, Table 1.3) was

the bivalve *Astarte* sp., which comprised 48% of the bivalves and 16% of the total fauna. The polychaetes *Prionospio steenstrupi* (16 % of polychaetes, 8% of total fauna), *Pholoe tecta* (14% of polychaetes, 7% of total fauna) and *Paradoneis lyra* (13% of polychaetes, 7% of total fauna) were the next most abundant taxa (Figure 1.4).

1.3.3 Species Abundance and Diversity

The most abundant species, *Astarte* sp., *Prionospio steenstrupi*, and *Paradoneis lyra* were abundant throughout the sampling period. The exception was *Pholoe tecta*, which increased in abundance (Figure 1.4, Table 1.3) later in the sampling period (Sept. and Oct.). With the exception of *Diastylis lucifera*, the abundances of all other dominant species increased towards the late summer and fall as did the variance (Figure 1.4). During the spring and early summer there was a low abundance of adult *Pholoe* (likely *P. tecta*) present, but a summer recruitment event resulted in an abundance of juveniles followed by a late summer / fall significant increase in the adult population of *Pholoe tecta* (Figure 1.4). There are two species of *Pholoe* in the study site, but *Pholoe minuta* (not shown in Figure 1.4) was unimportant in the PCA analysis (see below) and was generally much less abundant.

Univariate community measures (S, N, D, J, H' and ES[30]) (Figure 1.5) were not significantly different ($p > 0.05$) among sampling dates (Table 1.4), except for abundance which increased from spring through fall ($F_{(8,27)} = 2.01$, $p = 0.026$). The same data were then grouped into "seasons", based on CHN data, and were analysed using

one-way ANOVA with season as factor. This additional analysis confirmed the original conclusion that only abundance changed significantly ($F_{(3,30)} = 5.17$; $p = 0.005$) over the sampling period (Table 1.4). Mean rarefaction curves for each sample (Figure 1.6) showed variability within the sampling period but no temporal changes were significant when means and 95% confidence intervals were compared.

Regression analyses for environmental variables as predictors of macrofauna abundance and species richness revealed that sedimentary phaeopigments predicted abundance ($r^2 = 64.2$, $p = 0.030$) but not species richness ($r^2 = 43$, $p = 0.110$). No other variables, including sedimentary C, N, C/N and Chl-a, and water column variables, Chl-a and phaeopigments both surface and from depth were significant predictors of abundance and species richness (all $p > 0.05$) (Table 1.2).

1.3.4 Multivariate Analysis

In PCA analysis (Figure 1.7), the first two axes describe 25% of the variance, indicating high variability in faunal composition. For this analysis the two outlier samples (S17 and O14) were included. Gabriel biplots indicate which species contribute to the pattern and to what extent. The May 8 sample grouping is strongly characterized by the cumacean *Diastylis lucifera*. The June and July groups are characterized by the bivalve *Astarte* sp., and the fall group is characterized by the polychaete *Pholoe tecta*. A line has been added to the plot to indicate the seasonal progression of samples (Trueblood et al., 1994; Kelaher & Levinton, 2003).

Cluster analysis was consistent with PCA analysis in that spring samples (May 8 and May 21) were quite distinct from other samples. The samples from June (6th, 17th, and 28th) also clustered together though less distinctly suggesting that, this month may represent a transition phase into the remaining sampling period. Samples taken during July (23rd) formed the tightest group, this date represents the first significant increase in overall abundance (Figure 1.5). There is high variability in samples from August (28th), September (17th), and October (14th) which cluster together in mixed groups (Figure 1.8), suggesting spatial patchiness was more important than temporal changes during the late summer and fall.

1.4 DISCUSSION

Opportunism, variability in life-history characteristics, disturbances, detritus inputs, and recruitment events have been invoked to explain seasonal changes within benthic communities (Trueblood et al., 1994 and references therein; Kelaher & Levinton, 2003). Given the highly variable nature of species composition of nearshore benthic communities (McCall, 1977; Morrissey et al., 1992) and the variability of many environmental factors it is often hard to decipher which variable(s) contribute to observed changes.

Environmental variables examined here included sediment, water column pigments, and sediment CHN. Collectively they indicate moderate levels of food available to the

benthos in Bonne Bay (Figures 1.2 and 1.3). Traditional views of C/N ratios indicate that the food quality present varies from good to marginal (i.e. a ratio of 17 or higher is considered poor quality whereas 17 or lower is considered to be better quality (Hatcher, 1994 and references therein). C/N ratios in this study ranged between 8.02 and 16.4; which were slightly higher than those reported for another Newfoundland Bay (Ramey and Snelgrove, 2003). Stead and Thompson (2003) report sediment chlorophyll-a and phaeopigments in the range of 10-20 ng/mg and 30-60 ng/mg respectively in the deep depositional area (250-270 m) of Conception Bay, Newfoundland; the numbers from my study are considerably lower (0.0007-0.17 ng/mg and 0.6-1.5 ng/mg). Several factors may be responsible for the discrepancy. Export could be reduced by zooplankton grazing, especially in July and August when divers in the area have observed high numbers of visible gelatinous zooplankton (i.e. *Aurelia* sp., *Cyanea* sp., and ctenophores, pers. obs.). Organisms living in the sediment may process phytodetritus as quickly as it is deposited. Given the high abundance of deposit feeders, pigments may have been either consumed or reworked below the 1-1.5 cm mark where pigment samples were taken. It has previously been shown that the fate of sinking phytodetritus is strongly dependant on the macrofaunal community in the underlying sediment (Josefson et al., 2002), supporting the hypothesis that part of the sinking spring bloom is buried in the sediment before it is remineralized, digital pictures of experimental cores also support this hypothesis (pers. obs.). Furthermore, the cold temperatures (mean temperature was – 0.63 °C) in the Conception Bay study (Stead & Thompson, 2003) likely result in slow bacterial decomposition rates, resulting in longer persistence of sinking production

(Pomeroy & Diebel, 1986) than in the comparatively warm bottom water in Bonne Bay (2 °C to 14 °C, pers. obs.).

Multivariate analysis has become a powerful analytical method for large data sets, which are the norm for benthic ecology, where numbers of species can be in the hundreds (Ellis et al., 2000; and Ellis, 2003). A combination of multivariate analyses identified 4 faunal groups that were present during the sampling period; a May group, a June Group, a July group and a fall group. The May group is distinguished by the cumacean *Diastylis lucifera*, which has an abundance pattern that is quite distinct from most other species sampled. *D. lucifera* were most abundant during the spring and the fall, with low abundance in the summer months (Figure 1.4). This pattern is in contrast with most of the other species that are important in describing sample differences, such as *Pholoe tecta* and *Prionospio steenstrupi*. *Diastylis lucifera* is poorly studied but the congener, *D. rathkei*, displays a similar pattern in the Western Baltic Sea, albeit at higher abundances (Valentin & Anger, 1977). *D. rathkei* is thought to have declined from August to October because it is a major component of the diet of demersal fishes (Valentin & Anger, 1977). This explanation could apply here given that the abundance of demersal fishes (*Pseudopleuronectes americanus* and *Tautoglabrus adspersus*) greatly increased over the summer through the fall before declining toward the end of the sampling period (pers. obs.). Both species reduce feeding during the winter months (Scott & Scott, 1988); this reduction in predation pressure coupled with the abundance of phytoplankton as food (Yang, 1998) may explain high spring abundance of *D. lucifera*. In contrast both *P.*

tecta and *P. steenstrupi* occur in low abundance during the spring but increase in number over the summer through the fall (Figure 1.4). The predatory species, *P. tecta*, may increase when infaunal prey is abundant, and recruit into the system accordingly; *P. tecta* is known as an important infaunal predator in this arm of the bay (Quijon & Snelgrove, 2005).

The June group (comprised of $n = 3$ sampling dates) likely represents a transitional fauna between the spring group described above and the July group, which had the highest values of diversity (H') and the second highest abundances. This group was not strongly structured by any one species as indicated in the PCA analysis. The numerically dominant species, *Astarte* sp., *Paradoneis lyra*, and *Prioniospio steenstrupi* were dominant for all sampling dates and therefore did not contribute to variability among samples. *P. lyra* and *P. steenstrupi* are common species in sediments around Newfoundland and have been reported from shallow areas to depths of 2500-3000 m. *P. steenstrupi* has been reported as the numerically dominant taxon in several Atlantic benthic macrofaunal studies (Pocklington, unpublished). Both species belong to similar feeding guilds. *P. lyra* is a burrowing or surface deposit feeder, whereas *P. steenstrupi* is thought to be a surface deposit feeder. It is noteworthy, however, that members of this family (Spionidae) display a wide array of feeding strategies (Fauchald & Jumars, 1979) this may hinder an analysis of feeding guilds. The other dominant species of this group is the bivalve *Astarte* sp., which is a suspension feeder that lives near the sediment surface with part of its shell protruding into the water column (Widdicombe et al., 2004).

The July group is characterized by the bivalve *Astarte* sp. and a *Pholoe* sp. recruitment event (Figure 1.4); this was one of the few sampling dates where juveniles of this species were found. There was a significant difference in abundance in this group relative to previous sampling dates (Figure 1.5 and Table 1.4). Overall average abundance more than doubled from the previous two sampling times and then remained relatively constant for the remainder of the study period. This increase in abundance coincided with low levels of sedimentary carbon and nitrogen as well as low C/N ratios (Figures 1.2 and 1.3) that indicate higher food quality.

The fall group contained samples from August, September and October. This group is characterized by the polychaete *P. tecta*, which likely recruited to the cove in relatively high numbers in July. There is high variability within this sample group with respect to all univariate measures (Figure 1.5). Overall abundance peaked and then began to decline towards the end of the sampling period; a decline was also seen in all measures of biodiversity (H' , S , D , and $ES[30]$; Figure 1.5). The numerically dominant species included the polychaetes *P. lyra*, *P. steenstrupi*, and the bivalves *Astarte* sp. and *Crenella* sp. (Table 1.3). This group is similar in composition to the June group based on distribution of individuals among species but not in terms of abundances, which were consistently lower in June.

Univariate measures including Shannon-Weiner diversity, species richness and evenness were similar in value to those reported in another benthic study from Newfoundland (Ramey & Snelgrove, 2003). My results show that abundance increased significantly (Figure 1.5; Table 1.4) between the early months (May and June) and the later months (late July through October). This increase in abundance is primarily because of recruitment of *P. tecta* and *D. lucifera*. Throughout the sampling period, changes in diversity measures were not significant, although Shannon-Weiner diversity index, Margalef's Index, and species richness all peaked in July (Figure 1.5) and declined through the fall. This pattern suggests that abundance and diversity peak at the same time, when sedimentary carbon and nitrogen are at some of their lowest levels but food quality (as seen in the C/N ratio) was comparatively high. The following period (August) had the highest C/N ratio, indicating a poorer quality food source. Thistle (1981) suggested that as food quality declines, species composition may shift to species better adapted to lower organic carbon concentrations. This explanation is consistent with the change in faunal composition observed in late summer.

The data generally support the hypothesis that benthic communities change in response to variations food supply. The sediment pigment, carbon and nitrogen analysis indicate that there was a food pulse early in the sampling period, but the response was subtle and somewhat delayed. Biodiversity measures did not change significantly and abundance increases occurred months after the food pulse was detected. If recruits keyed in on this pulse it is possible that a 300 μm sieve may have missed initial recruits until they grew

large enough to be retained on the sieve (e.g. Schlacher & Wooldridge, 1996). A second food pulse was detected in early August, at a time when benthic faunal abundance was already high, in contrast with the arrival of the first food pulse. The response to this later food pulse was harder to interpret given that abundances were already high. Organisms that were already present could easily take advantage of this second pulse, particularly given the high quality of the organic matter (lower C/N ratios) and ready availability.

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Table 1.1: Comparisons of environmental variables from sediments and water column by one-way ANOVA with date as factor.

Environment	Dependent Variable	ANOVA's sources of Variation	
Water column		$F_{(7,8)}$	P
	Chl-a Surface	2.35	0.127
	Chl-a Depth ^a	37.79	0.001
	Phaeopigments surface	4.49	0.026
	Phaeopigments depth ^a	41.22	0.001
Sediment		$F_{(9,52)}$	P
	Carbon ^a	4.91	0.001
	Nitrogen ^a	3.32	0.003
	C/N ^a	4.64	0.001
	Chl-a	0.805 ^c	0.584
	Phaeopigments	12.61 ^b	0.001

^a Data log transformed.

^b Degrees of freedom (6,14).

^c P-value was calculated from randomly generated F-values (RF) with 500 iterations.

Table 1.2: Regression analysis of sedimentary and water column variables as predictors of abundance (N) and species richness (S) for each sampling date (n = 7). CHN Sampling did not occur on Sep. 21 and Jun. 28 and abundance data for those dates were therefore not included.

Environment	Dependent Variable	Regression Analysis			
		Abundance (N)		Species Richness (S)	
		r ²	p	r ²	p
Water Column ^a	Chl-a Surface	0.2	0.915	1.4	0.778
	Chl-a Depth ^b	7.1	0.563	8.3	0.530
	Phaeopigments	8.0	0.497	2.5	0.708
	Surface				
	Phaeopigments	14.9	0.393	16.0	0.374
	Depth ^b				
Sediment	Carbon	10.9	0.470	2.5	0.734
	Nitrogen	7.1	0.723	1.1	0.823
	C/N	8	0.318	0.9	0.839
	Chl-a	14.9	0.359	41.3	0.120
	Phaeopigments	64.2	0.030	43	0.110

^a Water sampling occurred on Sep. 21 therefore n = 8 for water analysis.

^b Outlier (May 21) was removed from analysis.

Table 1.3: Mean abundance (organisms / 38.5 cm²) \pm 95% confidence intervals of numerically dominant fauna per sampling date sorted by month (May, n = 8; June, n = 12; July, August, n = 4; September and October, n = 3).

Rank	Taxa and densities per sampling date per month											
	May		June		July		August		September		October	
1	<i>Diastylis lucifera</i>	8.13 \pm 3.89	<i>Astarte</i> sp.	14.25 \pm 4.6	<i>Astarte</i> sp.	15.25 \pm 7.6	<i>Pholoe tecta</i>	13.8 \pm 7.64	<i>Astarte</i> sp.	23 \pm 16.04	<i>Astarte</i> sp.	15.3 \pm 7.1
2	<i>Paradoneis lyra</i>	5.13 \pm 2.04	<i>Paradoneis lyra</i>	5.3 \pm 1.1	<i>Prionospio steenstrupi</i>	12.8 \pm 3.78	<i>Astarte</i> sp.	12.8 \pm 4.69	<i>Crenella</i> sp.	13.6 \pm 8.34	<i>Pholoe tecta</i>	14.6 \pm 7.7
3	<i>Prionospio steenstrupi</i>	4.25 \pm 2.18	<i>Prionospio steenstrupi</i>	5.2 \pm 1.7	<i>Pholoe</i> juvenile	12.3 \pm 12.0	<i>Prionospio steenstrupi</i>	9.75 \pm 4.95	<i>Pholoe tecta</i>	12.6 \pm 8.49	<i>Paradoneis lyra</i>	8 \pm 5.18
4	<i>Astarte</i> sp.	3.5 \pm 0.97	<i>Crenella</i> sp.	4.9 \pm 2.1	<i>Pholoe tecta</i>	6.75 \pm 4.89	<i>Diastylis lucifera</i>	8 \pm 7.33	<i>Prionospio steenstrupi</i>	9.3 \pm 8.49	<i>Prionospio steenstrupi</i>	6.3 \pm 4.57
5	<i>Macoma</i> sp.	2 \pm 1.43	<i>Thyasira</i> sp.	1.9 \pm 0.97	<i>Crenella</i> sp.	5.5 \pm 2.46	<i>Cerastoderma</i> sp.	5.75 \pm 6.26	<i>Asebellides lineata</i>	7.6 \pm 12.2	<i>Cerastoderma</i> sp.	5.6 \pm 4.7
6	<i>Cerastoderma</i> sp.	1.88 \pm 0.86	<i>Pholoe tecta</i>	1.75 \pm 0.84	<i>Amphaertidae</i> juvenile.	5 \pm 8.54	<i>Paradoneis lyra</i>	5.5 \pm 0.97	<i>Paradoneis lyra</i>	6.3 \pm 3.97	<i>Tharyx</i> sp.	4.33 \pm 7.53
7	<i>Crenella</i> sp.	1.63 \pm 1.04	<i>Cerastoderma</i> sp.	1.6 \pm 0.77	<i>Macoma</i> sp.	3 \pm 0.8	<i>Crenella</i> sp.	5 \pm 3.2	<i>Diastylis lucifera</i>	4.6 \pm 5.1	<i>Chone duneri</i>	3.33 \pm 1.72
8	<i>Pygospio elegans</i>	1.25 \pm 1.44	<i>Chone duneri</i>	1.4 \pm 0.65	<i>Pectinaria granulata</i>	2.75 \pm 1.67	<i>Macoma</i> sp.	4.75 \pm 2.44	<i>Chone duneri</i>	3.6 \pm 0.65	<i>Diastylis lucifera</i>	2.66 \pm 1.3
9	<i>Chone duneri</i>	1.13 \pm 0.78	<i>Bathymedon</i> sp.	1.25 \pm 0.93	<i>Phyllodoce mucosa</i>	2.5 \pm 2.3	<i>Diastylis sculpta</i>	4.5 \pm 4.04	<i>Scoloplos armiger</i>	3.33 \pm 2.35	<i>Diastylis sculpta</i>	2.0 \pm 2.99
10	<i>Aricidea catherinae</i>	1 \pm 0.74	<i>Euchone papillosa</i>	1.1 \pm 0.53	<i>Asabellides lineata</i>	2.25 \pm 2.57	<i>Asabellides lineata</i>	4.25 \pm 1.85	<i>Euchone papillosa</i>	2.66 \pm 1.13	<i>Strongylocentrotus droebachiensis</i>	1.66 \pm 2.35
Totals	May	46.13 \pm 6.48	June	47 \pm 6.13	July	108 \pm 19.22	August	99.5 \pm 30.6	September	123.3 \pm 59.7	October	95 \pm 38.6

Table 1.4: Analysis of univariate benthic community parameters by one-way ANOVAs with sampling date and season as factors.

Dependent Variable	ANOVA's sources of variation			
	Sampling Date (n = 9)		Season (n = 4)	
	F _(8,27)	P	F _(3,30)	P
Abundance (N) ^a	2.01 ^b	0.026	5.17	0.005
Species Richness (S)	2.02	0.080	1.02	0.399
Evenness (J)	1.21	0.330	0.48	0.701
ES(30)	1.34	0.458	1.10	0.363
Shannon-Weiner (H')	1.02 ^b	0.436	0.21	0.886
Margalef's Index (D)	1.58	0.178	0.35	0.791

^a Abundance data for season analysis was log transformed.

^b P-values were calculated from randomly generated F-values with 500 iterations.

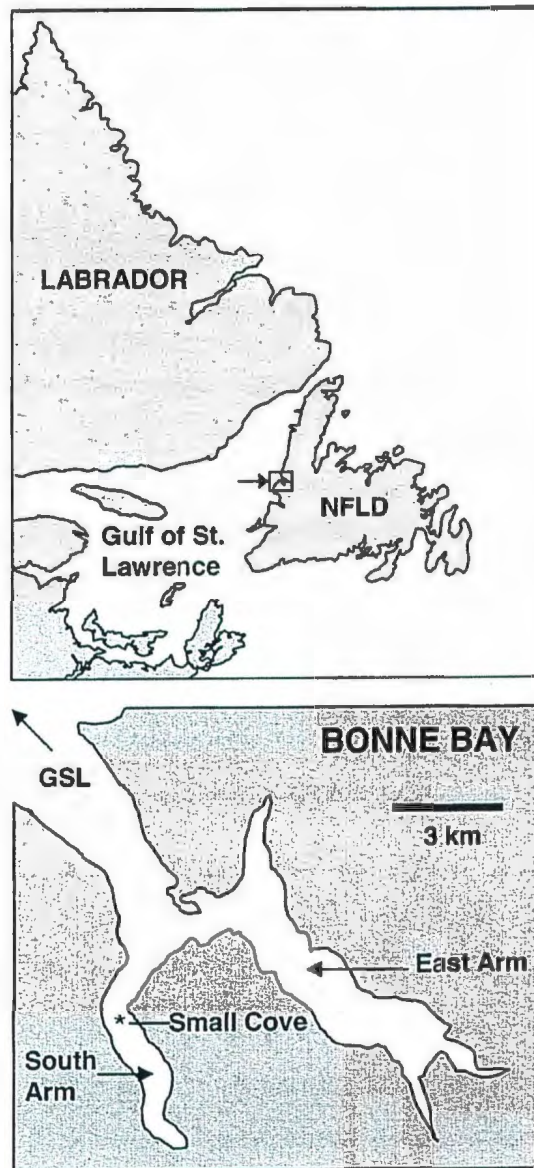


Figure 1.1: Location of Bonne Bay, Newfoundland (top). Layout of Bonne Bay, including East and South Arms as well as Small Cove (sampling site – star; bottom).

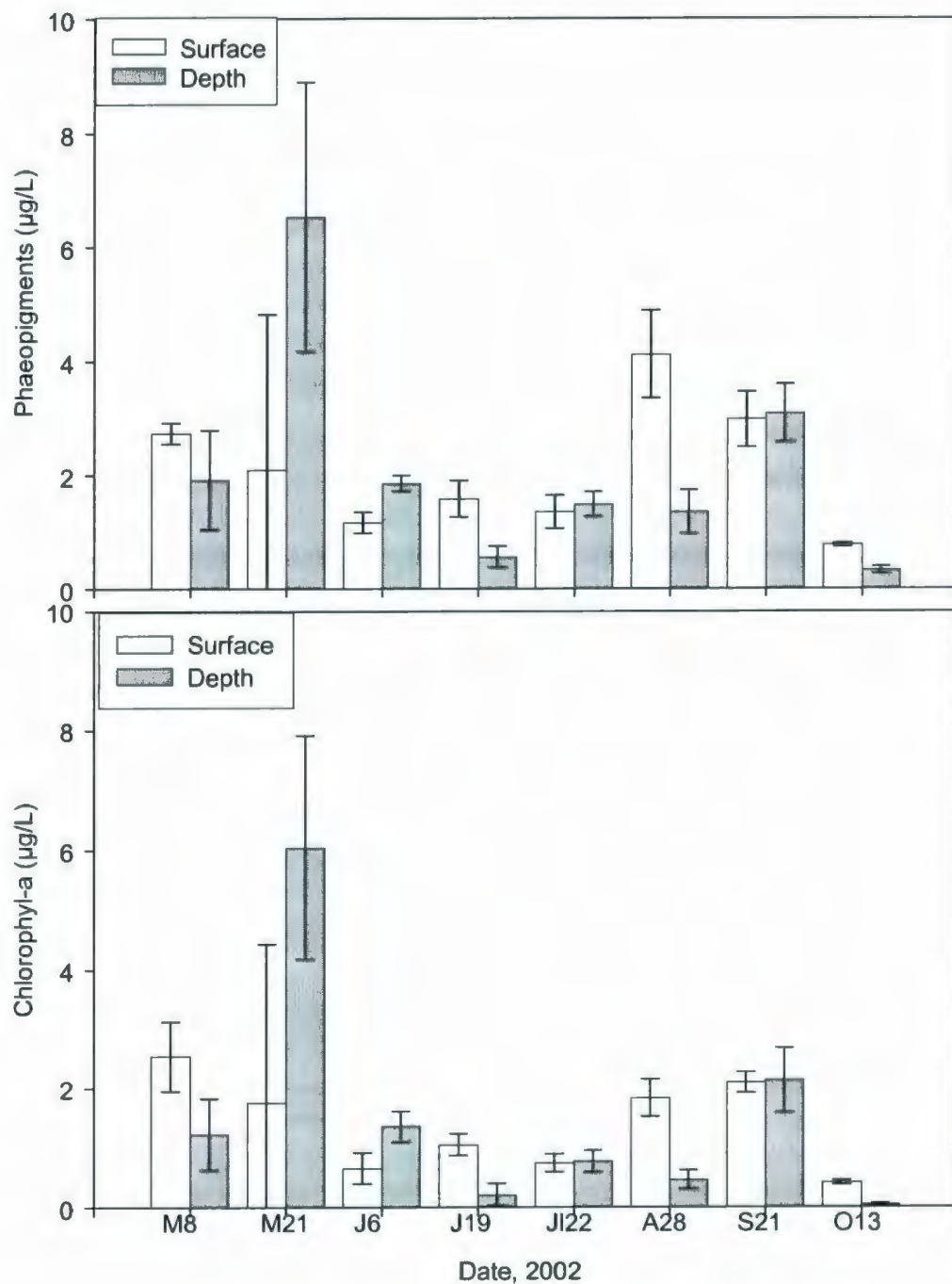


Figure 1.2: Water column chlorophyll-a and phaeopigments concentrations (means and 95% confidence intervals) for each sampling date. Samples from depth were collected at ca. 19 m. M8 = May 8; M21 = May 21; J6 = June 6; J19 = June 19; J122 = July 22; A28 = August 28; S21 = September 21; and O13 = October 13.

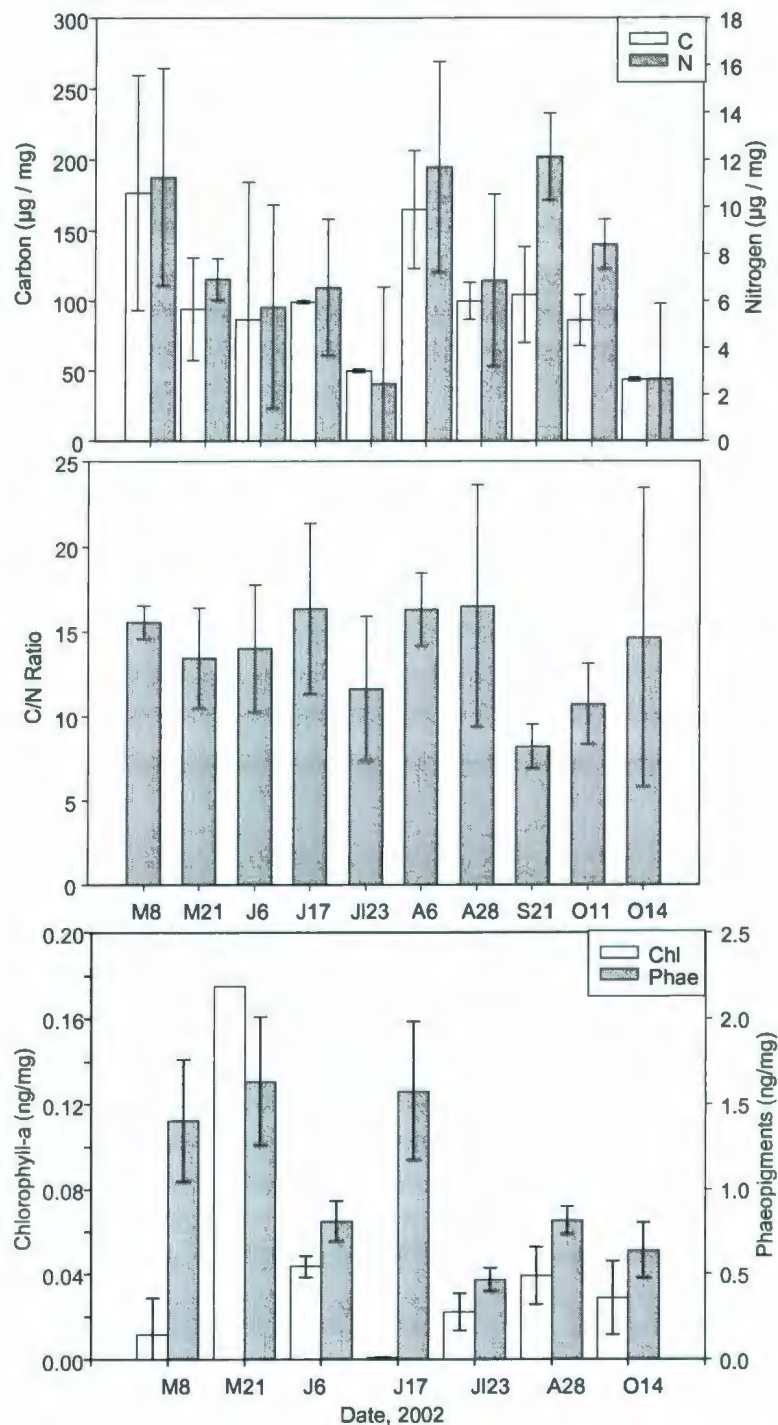


Figure 1.3: Sediment parameters (means and 95% confidence intervals): A) Carbon and nitrogen values; B) C/N ratio (by weight), where $n = 2$, except for August 6th, September 21, and October 11th, where $n = 16$; C) Chlorophyll-a and phaeopigments, where $n = 3$; for each sampling date.

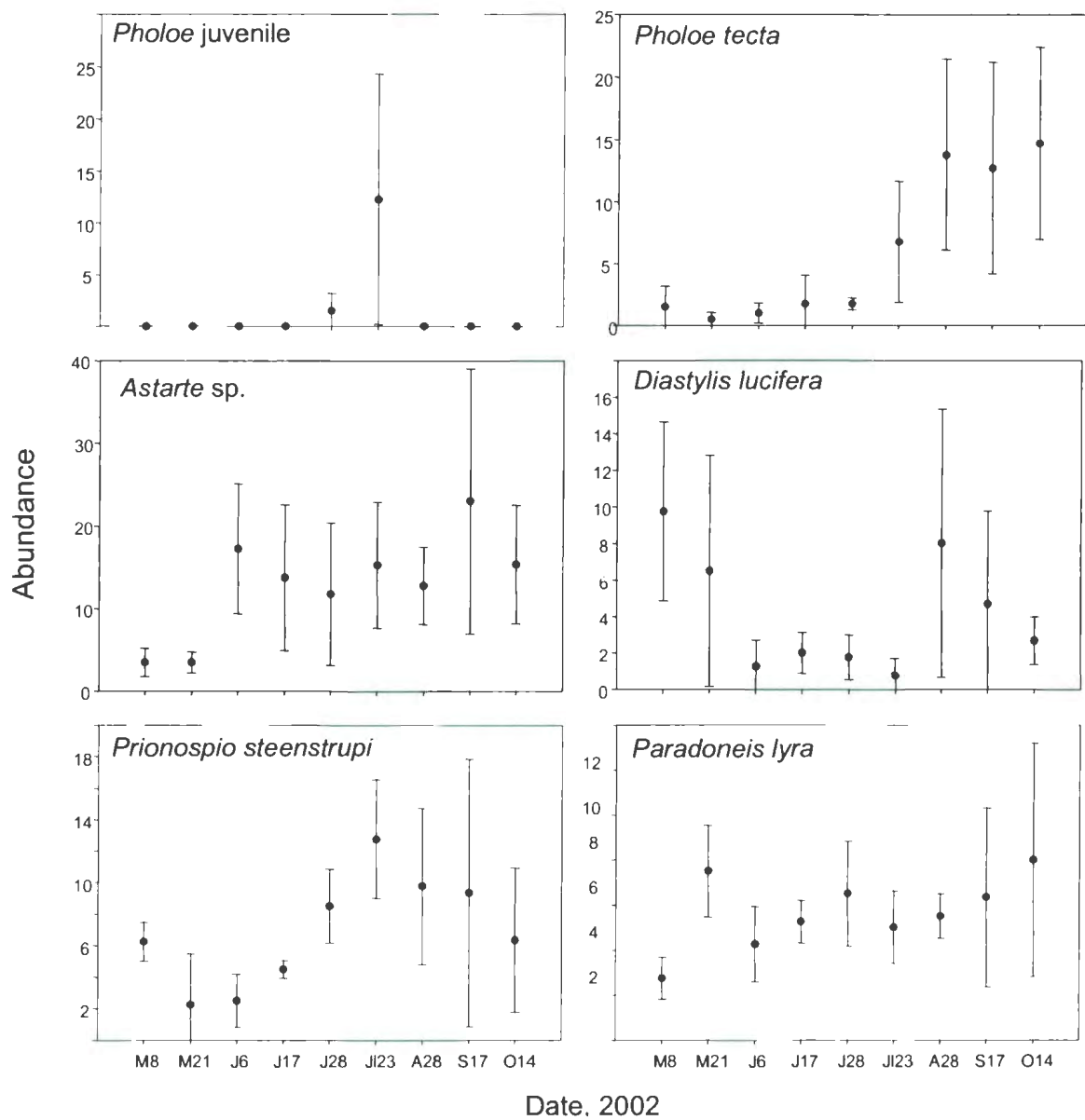


Figure 1.4: Mean abundance (n = 4 replicates; except for S17 & O14, n = 3 replicates) and 95% confidence intervals for numerically dominant and important species identified from PCA-H analysis for each sampling date. See Fig. 1.2 for explanation of date abbreviations.

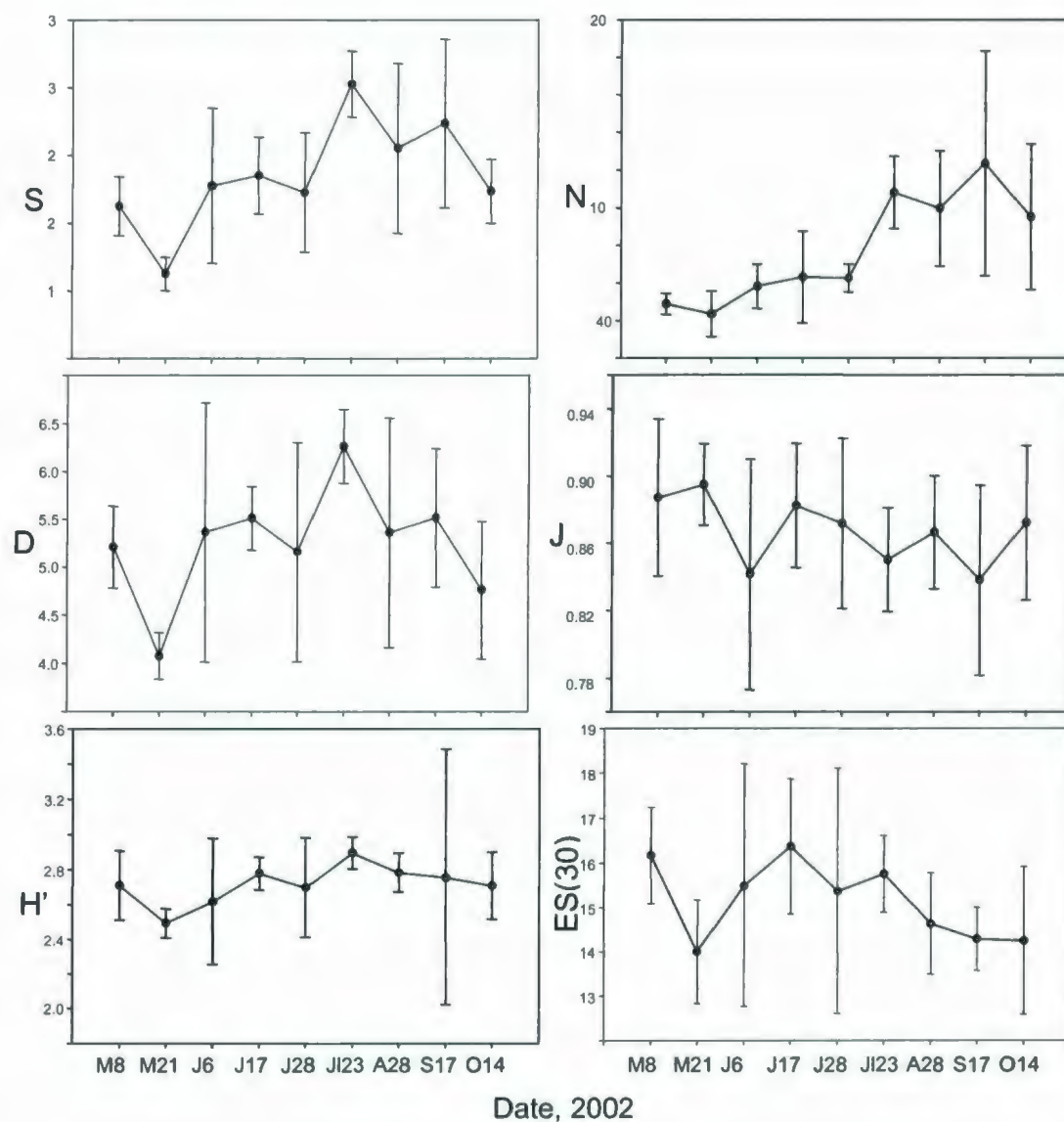


Figure 1 5: Univariate community measures for each sampling date (means and 95% confidence intervals. Note Y-axes change scale. N = abundance, S = Species richness, D = Margalef's Index, J = Evenness, H' = Shannon-Weiner Diversity Index, and ES(30) = Expected Species Shared (n = 30). See Fig. 1.2 for explanation of date abbreviations (n = 9 dates; n = 4 replicates, except for S17 & O14 where n = 3).

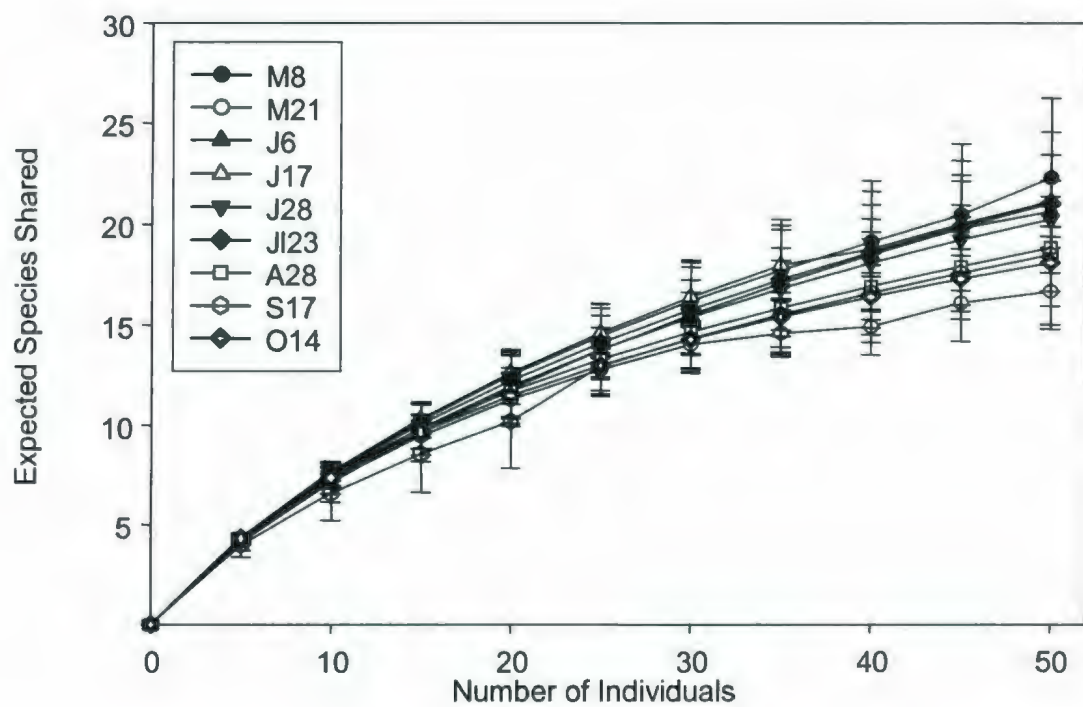


Figure 1 6: Rarefaction curves (95% confidence intervals) for means of cores from each sampling date (n = 4). See Fig. 1.2 for explanation of date abbreviations.

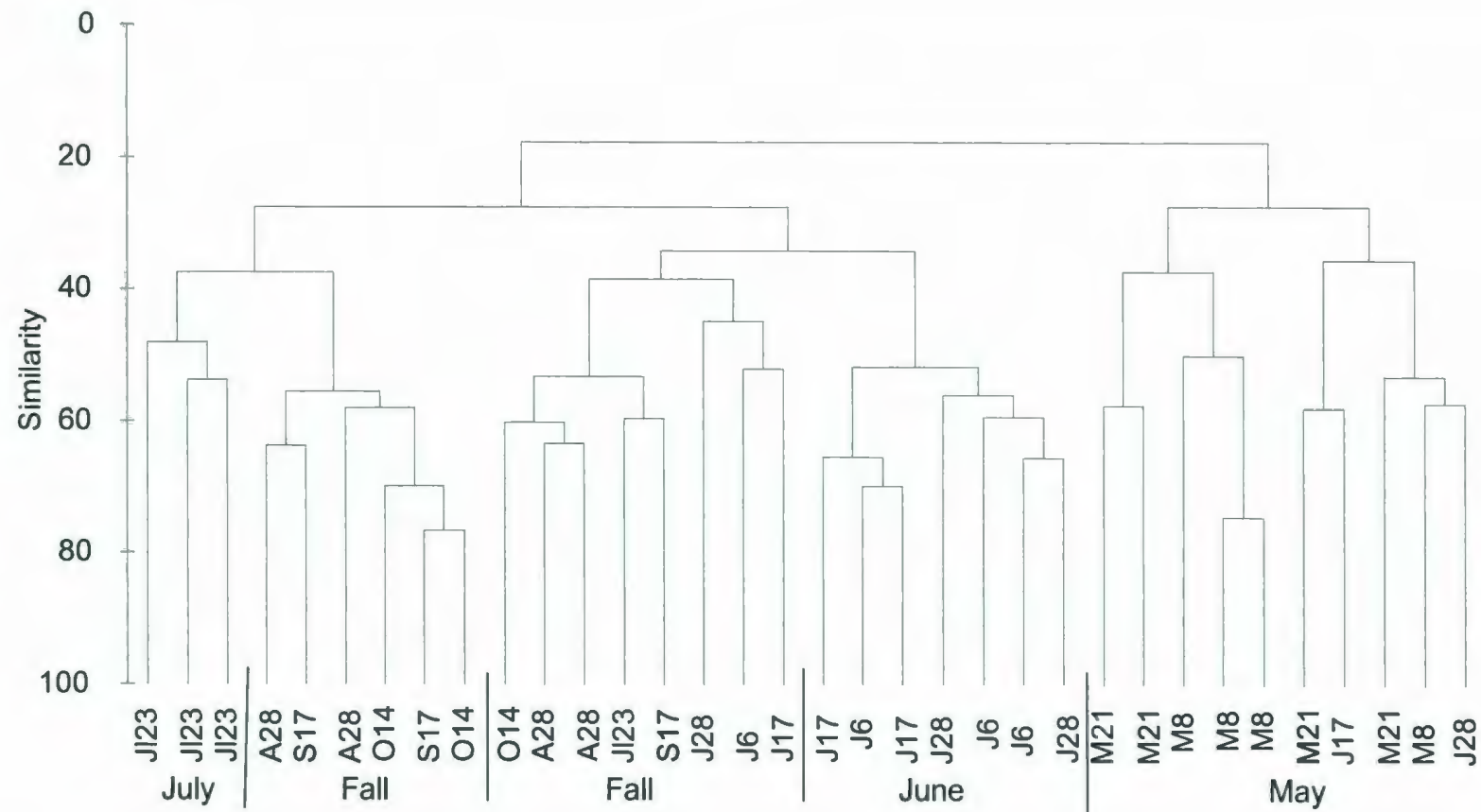


Figure 1 8: Cluster analysis of Bray-Curtis similarity matrix of untransformed data using complete linkages for all sampling dates and replicates. See Fig. 1.2 for explanation of date abbreviation.

CHAPTER 2

IMPORTANCE OF COMPOSITION AND DIVERSITY OF PHYTODETRITAL FOOD SUPPLY FOR BENTHIC SEDIMENTARY MACROFAUNAL COMMUNITIES IN A NEWFOUNDLAND FJORD

This chapter has been submitted and conditionally accepted by Marine Ecology Progress Series. It will be resubmitted with edits in the upcoming months.

2.1 INTRODUCTION

Our understanding of biodiversity in marine sediments is limited in many respects mainly because of undersampling of one of the Earth's largest ecosystems, and the myriad variables that influence benthic sedimentary communities (Snelgrove & Butman 1994). In coastal areas, habitat heterogeneity (Grassle & Grassle 1992), historical effects (Gray 2002) and nearshore disturbances such as storms (Norkko et al. 2002) and winds (Commito et al. 1995) are among the variables that can contribute to biodiversity patterns. Studies are lacking, however, on the effect that diversity of food supply has on the maintenance or promotion of sedimentary biodiversity in shallow-water sedimentary communities.

Much of the food supply for subtidal benthic organisms is derived from the overlying water column (Billett et al. 1983; Graf 1992; Josefson & Conley 1997; Parrish 1998); at temperate latitudes a significant part of this material may originate from the spring phytoplankton bloom (Smith et al. 2001). Multiple studies have documented marked pulses in labile organic matter shortly after the spring bloom both in shallow (e.g. Graf et al. 1982; Bertuzzi et al. 1996) and deep-sea (e.g. Billett et al. 1983) areas. In some cases the sunken phytodetritus can form a greenish "carpet" at the sediment-water interface

(Smetacek 1984). Measurements of heat production, oxygen demand and temperature show a strong benthic response during and after a sinking bloom in Kiel Bight (Graf et al. 1982), but effects of natural bloom events on sedimentary biodiversity are poorly known. Given that not all organic matter that reaches the bottom is immediately available to benthic macrofauna, and that food supply is an important factor in regulation of some benthic communities, how does the composition of the food supply influence benthic community structure?

In order to understand how food supply might influence benthic community structure, the composition of sinking organic material must be understood. Sinking particles in the ocean have been well studied (e.g. Billett et al. 1983; 1985; Fowler & Knauer 1986; Alldredge & Silver 1988; Grebmeier & McRoy 1989; Parrish 1998; Smith et al. 2001). Sinking material can comprise both living and dead organisms, parts of organisms, or waste products from animals. These small individual components can sink separately or form tiny ($> 500 \mu\text{m}$) aggregations of marine snow that are important microhabitats for pelagic bacteria and protists (Alldredge & Silver 1988). The quality of sinking material as a food source for benthic organisms depends on its composition. For example, in temperate and sub-arctic ecosystems, the spring bloom is composed primarily of diatoms, which can sink to the seafloor as intact cells. For shallow-water environments in particular, these intact cells provide a high-quality food source that is readily incorporated into benthic food webs (Graf 1992; Parrish 1998). This availability is in contrast with structurally complex plant material such as leaf litter that has high cellulose

and lignin content, which is of limited nutritional value and consequently a poorer quality food source (Kendall et al. 1995). Intact phytodetritus cells can easily be incorporated directly into the food chain through ingestion, or they may be quickly mixed below the sediment-water interface for later use (Josefson et al. 2002; Witte et al. 2003). Levin et al. (1999) found that on the North Carolina continental slope that phytodetritus is consumed quickly by protozoans and metazoans, in hours to days, or alternatively it may be buried, cached or worked into the sediment by animal activities, in particular large bioturbators. Within the same study it was found that surface deposit feeders consistently showed higher loads of tracer, indicating that a significant portion of feeding takes place at the sediment surface (Levin et al. 1999).

A few studies have focused on the response of shallow-water macrofauna to supply of phytodetrital organic matter (Kendall et al. 1995; Josefson & Conley 1997; Stocks & Grassle 2001; Kelaher & Levinton 2003). In most cases the faunal response has been quick (days to months; Kelaher & Levinton 2003). Most of these studies have focused on intertidal mudflats or saltmarsh ecosystems and comparatively little is known for shallow-water subtidal communities (Stocks & Grassle 2001; Quijon et al., 2008).

One method of evaluating response to organic material is to enrich sediment within an experimental tray containing sediments, which is then deployed onto/into the seafloor; after some period of time the tray is recovered (e.g. Snelgrove et al. 1992; Kline & Stekoll 2001). Tray experiments have the advantage of simplifying interacting variables

such as predation and adult-larval interactions that could influence faunal response to sediment enrichments but biases can be introduced by altering bottom flow (Snelgrove et al. 1992), excluding horizontal colonizers, and altering sediment geochemistry (Smith & Brumsickle 1989). A more natural experimental approach would be to enrich the natural seafloor, and thereby mimic phytodetritus flux to the seafloor. Very few studies have attempted *in situ* enrichment of intact sediments (deep-sea e.g. Witte et al. 2003). *In situ* benthic enrichment experiments add realism by encompassing the complexity of the natural ecological interactions within the community (Grassle et al. 1980), sediment geochemistry is not disrupted, and more species are included within the species pool (Kline & Stekoll 2001). The disadvantages of *in situ* experiments include complex logistics; except for submersibles and related technologies, sub-tidal habitats are only accessible by divers and are therefore limited to relatively small scales. The complexity of ecological interactions tends to produce large variation within the results, necessitating large numbers of replicates (Kline & Stekoll 2001).

Few studies have examined the role of organic composition on faunal response, and the studies that have examined this question have focused primarily on the deep-sea (Snelgrove et al. 1992; 1996). Similar studies are lacking for shallow-water systems. In this study, *in situ* experiments are used in an attempt to examine the potential effect of the composition and diversity of sinking food supply (phytodetritus) on a shallow-water soft-sediment community. Specifically, I ask whether different types of phytodetritus attract different suites of species and diversity of colonizing species, and does a diverse

food source attract a greater diversity of colonizers and therefore higher abundances of different species when compared with relatively homogeneous food sources?

2.2 MATERIALS AND METHODS

2.2.1 Sampling Site

Experiments were deployed in “Small Cove”, in the South Arm of Bonne Bay, Newfoundland (Figure 1.1). Bonne Bay is a fjord on the Northwest coast of Newfoundland (the study site is further described in the thesis introduction as well as Quijon & Snelgrove 2005). Experiments were carried out in the summer and fall of 2002 along two transect lines within the cove at a depth of ~20 m. The summer transect line ran between 49°28.872 N 57°54.551 W and 49°28.837 N 57°54.481 W and the fall transect line ran between 49°28.840 N 57°54.485 W and 49°28.798 N 57°54.472 W.

2.2.2 Establishing Artificial Patches

Artificial patches were created by gently placing an inverted (open bottom) clear plastic container (38 cm x 26 cm x 13 cm high) on the sediment surface by divers for a period of 24 hours at a depth of 20 m. The chambers were not pushed into sediment to avoid creating a “footprint” which could disturb flow over the patch during the experiment; the chambers were weighted to prevent them from floating away. Prior to deployment small 0.5 cm holes were drilled in the top and high on the sides of the container to act as vents. In addition, a 0.75 cm hole was drilled in the sides of the container and hollow plastic tubing was glued to the hole and across the inside of the container. Multiple tiny holes were drilled into the tubing along its length to create a “spray bar” that would disperse

the algal treatment throughout the interior of the container. Assembled containers were soaked on site for at least 24 hours before deployment on the sediment.

Algal treatments (Instant-Algae® from Reed Mariculture) were transported to the bottom in pre-calibrated syringes that were attached to the spray-bar prior to gently injecting the algae into the chamber. The syringe was reloaded with ambient seawater and again injected to flush any remaining treatment from the syringe and spray bar. For control treatments, ambient seawater only was injected into chambers instead of algae. The chamber was left in place for an additional 24 hours to allow the algae to settle on the sediment before it was gently removed and experiments were initiated.

2.2.3 Experiments

For each experiment (summer and fall) 20 artificial patches were created along two transect lines using 5 different treatments: (1) A monoculture of *Thalassiosira weissflogii* (Bacillariophyceae, a large centric diatom hereafter *Thalassiosira*) (2) A monoculture of *Chaetoceros gracilis* (Bacillariophyceae, a chain-forming diatom hereafter *Chaetoceros*) (3) A monoculture of *Nannochloropsis* sp. (Eustigmatophyceae, a small green algae, hereafter *Nannochloropsis*) (4) A mixture of *Thalassiosira*, *Chaetoceros*, and *Nannochloropsis* (5) No enrichment (seawater only).

Each treatment was replicated 4 times along the transect line and treatments were haphazardly interspersed at 1 – 3 m intervals.

The amount of algae added for each treatment was equivalent to carbon accumulation for 35 days (the approximate duration of the experiment) at peak spring bloom levels as measured in three Newfoundland bays: Trinity Bay (Parrish 1998) Conception Bay (Redden 1994), and Bonne Bay (Tian et al. 2001). This amount was estimated to be 18.55 g m^{-2} of organic material or 1.81 g when scaled to patch size. The volume of each culture to be delivered was determined based on dry weight, as well as the assumption that organic material was 30% carbon, so that 6.04 g of carbon was added for each treatment. Because the dry weights of each culture differed, 31 to 127 ml of culture was necessary to deliver the desired amount of carbon. For the mixture treatment, 6.04 g C was apportioned among the 3 algal species, and the appropriate proportions were mixed together in a large beaker prior to loading into syringes. Algal cultures were refrigerated at 5 °C (for a period not exceeding 2 weeks) until the day they were measured and loaded into syringes. Treatment 5 (no enrichment) served as a control for syringing and container effects. Each patch was sampled approximately one week after enrichment with a single sediment core (diameter of 6.5 cm, pushed to a depth of approximately 10 cm), then again approximately four weeks later (5 weeks after enrichment) for a total of 40 cores per experiment. Cores were sectioned into 0-2 cm, 2-5 cm, and 5-10 cm strata. The sections were sieved on a 300- μm sieve, washed with filtered seawater, placed into glass sample jars and fixed in 10% buffered formalin solution for at least 24 hours. They were subsequently rinsed back into glass jars with 70% alcohol and stained with Rose Bengal. Samples (top 5 cm) were sorted and organisms were identified to the lowest possible taxon, which was usually species. Juveniles were individuals that were

recognizable as smaller than adults, but lacked distinguishing characteristics to be positively identified as an adult or to genus and species. Therefore juveniles were only identified to the lowest possible taxon. Representative samples from the 5-10 cm sediment strata were also sorted, but because 99.5% of organisms were found in the top 5 cm, the remaining samples from the 5-10 cm fraction were not sorted and the fraction was not included in analyses. This entire experiment was carried out once during the summer and once during the fall of 2002. The first experimental enrichment (summer, 40 cores) began June 20th, and was sampled on June 30th and again on July 26th. The second experiment (fall, 40 cores) began on Aug 24th, and was sampled on September 8th and again on October 9th 2002. Because the *Chaetoceros* algal culture was unavailable, *Tetraselmis* sp. (Chlamydomonadaceae, a large green flagellate hereafter *Tetraselmis*) was substituted for the fall experiment. The resulting treatments for the fall experiment were as follows: (1) A monoculture of *Thalassiosira* (2) A monoculture of *Tetraselmis* (3) A monoculture of *Nannochloropsis* (4) A mixture of *Thalassiosira*, *Tetraselmis*, and *Nannochloropsis* and (5) No enrichment.

In a few instances during the fall experiment, one of the plastic containers was missing upon return to the site to inject algal treatments. In these instances, the affected patches were prepared again, following the same protocol; each patch was sampled within the same time frame as those originally enriched except that they were offset by several days. For this reason I included the data from these patches with the original patches for data analysis.

2.2.4 CHN Sampling

Mini-cores (60 ml syringes with tip removed) were pushed 2-3 centimetres into the sediment to sample sediment for CHN analysis. The top 1 cm was removed from each core, and frozen until analysis. Samples were then freeze-dried at -60 °C and analyzed in duplicate using a Perkin-Elmer Model 2400 CHN Analyzer. Samples were taken during the July 26th, September 8th, and October 9th sampling dates for a total of 60 samples.

2.2.5 Data Analysis.

Because the algal treatments differed between experiments, and a strong seasonal signal in the ambient fauna was present (Chapter 1) it was inappropriate to analyze the data from both experiments in one analysis. Data from each experiment were therefore analysed separately using univariate and multivariate methods.

Primer v5 was used to generate univariate community measures, abundance (N), species richness (S), Margalef's biodiversity index (D), evenness (J), Shannon-Weiner diversity index (H'), and Expected Species (based on 30 individuals) ES[30]. Means and 95% confidence intervals were plotted for each measure. For statistical comparison, the residuals of these measures were first analysed for normality using a Ryan-Joiner Normality test and homogeneity of variance was tested using Levene's test of equality of error variances. If the assumptions were met then data were analysed using two-way ANOVA with time and treatment as factors. Where data did not meet these assumptions, the data were log transformed. If transformation did not resolve the problem, F-values

were generated by means of randomization with 500 iterations with replacement. From these random F-values, p-values were calculated.

Hurlbert rarefaction curves (Hurlbert, 1971) were generated using Primer v5; curves were plotted using means of replicates and 95% confidence intervals for each treatment and sampling period. Rarefaction curves were further analysed by means of ANCOVA with week and treatment as factors and number of individuals as a covariate. In all cases a polynomial regression transformation was used to ensure assumptions of ANCOVA were met.

Chord Normalized Expected Species Shared (CNESS), with $m = 10$ individuals was used to compare similarity of communities for each sampling week (20 cores), as well as for all of the samples in a given experiment (40 cores). CNESS was selected because of its ability to deal with rare species. Principal Components Analysis (PCA) based on the CNESS similarity matrix was overlaid with Gabriel biplots that identified those species driving similarity patterns.

CHN measurements were plotted and compared by means and 95% confidence intervals as well as by one-way-ANOVA with treatment as factor. Time could not be tested because sediments for CHN were only sampled in week 5 for the summer experiment. CHN data for the fall experiment was compared using a two-way ANOVA with treatment and time as factors. One replicate measurement of carbon was highly

anomalous within the fall experiment and was therefore discarded, resulting in an unbalanced ANOVA. To compensate for this missing value, the average of the remaining 3 replicates was substituted, and one degree of freedom was subtracted from the overall error (Underwood 1996).

2.3 RESULTS

2.3.1 *Experimental Fauna Overview*

A total of 2364 and 2751 individuals were recorded from the summer and fall experiments respectively; total abundance for each sampling week ranged from 967 to 1401 individuals. Of the 106 taxa identified, polychaetes were the dominant group ranging from 55% to 64% of the total individuals for a given sampling period; other groups included molluscs, anthozoans, hydrozoans, crustaceans, nemerteans, sipunculids and echinoderms. Bivalve molluscs made up 21% and 29% of the total individuals from the summer and fall experiments respectively; all other groups combined made up 18% and 14% respectively. The fauna exhibited a relatively high level of dominance. For example, the top 5 taxa for any given sampling week generally made up 50% of the total abundance; the most abundant taxa included the polychaetes *Paradoneis lyra*, *Prionospio steenstrupi*, *Pholoe tecta*, the cumacean *Diastylis lucifera*, the bivalves *Astarte* sp., *Crenella* sp. *Cerastoderma* sp., and the amphipod *Bathymedon* sp. (Tables 2.1a and b). Juvenile *P. tecta* polychaetes and juvenile cumaceans were among the most abundant taxa for week 5 of the summer experiment, however, juveniles were not encountered in any other sampling period.

2.3.2 Diversity Measures

Two-way analysis of variance of either species richness (S), abundance (N), Margalef's Index (D), evenness (J), or Shannon-Weiner diversity index (H') were compared with treatment and time as factors revealed different results for the different experiments. The only measure that was significantly different among treatments was evenness (J) for the fall experiment ($F_{(4,30)} = 3.051$; $p = 0.03$); where the *Tetraselmis* treatment was significantly different from the *Nannochloropsis* treatment. For the summer experiment species richness (S; $F_{(1,30)} = 8.534$, $p = 0.007$), abundance (N; $F_{(1,30)} = 4.074$, $p = 0.038$) and Margalef's index (D; $F_{(1,30)} = 7.816$, $p = 0.009$) were significantly higher for week 5 of the experiment, but none differed with respect to treatment. In the fall experiment, no measures were significantly different with respect to time. Interaction terms were not significant for any measure in either experiment.

Although no differences were observed in Expected Species for $n = 30$ individuals ($p > 0.05$; for both experiments, all treatments, weeks and interaction terms), in the summer experiment rarefaction curves for the treatments and the control intermingled for week 1, however by week 5 the control and the algal treatments diverged, this is significant ($F_{(4,74)} = 14.953$, $p < 0.001$) indicating higher diversity values for the algal treatments during the later summer (Figure 2.1a and b) relative to controls. To some extent this trend was reversed in the fall experiment; rarefaction curves for week 1 treatments were slightly elevated relative to controls, but by week 5 the curves were intermingled (Figure

2.1c and d) no significant differences were detected by ANCOVA analysis ($F_{(4,90)} = 0.509$, $p = 0.729$).

2.3.3 Multivariate Analysis

Principal Components Analysis (PCA) of the summer experiment clearly distinguished the two sampling weeks along the PC1 axis, however, there was no pattern with respect to experimental treatments. Three of 4 control (X) replicates for both sampling weeks consistently grouped together, but in both cases these control samples clustered with the mixture treatments. A similar analysis for the fall experiment did not clearly distinguish between sampling weeks, and nor did any treatments group together consistently (Figure 2.2). In separate analyses of each week of each experiment, during week 1 of the summer experiment the *Thalassiosira* treatment separated from the other algal treatments and control treatment, along the PC2 axis. This pattern did not persist to the fifth week, when the separation of the *Thalassiosira* treatments was no longer observed (Figure 2.3). For the fall experiment during week 1, the PC2 axis again separated the *Thalassiosira* treatments from the other treatments and controls. In this instance the polychaete *Phyllodoce mucosa* contributed strongly to the pattern. By the fifth week, this separation was no longer apparent, although the polychaete *P. mucosa* continued to drive community pattern, though not just *Thalassiosira* treatments. During this sampling week, the algal mixture treatment (M) formed a tight grouping driven primarily by the bivalve *Crenella* sp. (Figure 2.3).

2.3.4 Carbon and Nitrogen Analysis

Analysis of variance for carbon and nitrogen variables indicated no significant differences between treatments for week 5 of the summer experiment for carbon ($\bar{x} = 170.6 \mu\text{g/mg}$; $F_{(4,15)} = 1.94$; $p = 0.156$), nitrogen ($\bar{x} = 11.2 \mu\text{g/mg}$; $F_{(4,15)} = 1.54$; $p = 0.240$) and C/N ratio ($\bar{x} = 17.1$; $F_{(4,15)} = 0.254$; $p = 0.903$) (Figure 2.4). For the fall experiment, no significant differences were found between treatments (C, $\bar{x} = 89.8 \mu\text{g/mg}$; $F_{(4,29)} = 1.02$; $p = 0.476$; N, $\bar{x} = 9.1 \mu\text{g/mg}$; $F_{(4,29)} = 0.556$; $p = 0.697$; C/N, $\bar{x} = 10.5 \mu\text{g/mg}$; $F_{(4,29)} = 0.664$; $p = 0.622$). However, because sampling for carbon and nitrogen was carried out for both sampling weeks, differences were significant with time as a factor for N ($F_{(1,29)} = 28.991$ $p = 0.000$) and C/N ($F_{(1,29)} = 13.822$ $p = 0.001$). Nitrogen values were higher during week 1 whereas C/N values were higher in week 5 (Figure 2.4). Carbon levels ($F_{(2,44)} = 10.869$, $p < 0.001$) as well as C/N ratios ($F_{(2,43)} = 19.998$, $p < 0.001$) were significantly higher in the summer experiment than during either week of the fall experiment (Figure 2.4).

2.4 DISCUSSION

The objectives of this chapter were to determine if changes in available food supply can elicit different community patterns within the benthic macrofauna. To do this I created artificial patches on the seafloor in hopes of mimicking patchy settled phytodetritus of different species and a mixture of species. The species chosen were had slightly different attributes. There were two diatoms (*Chaetoceros* and *Thalassiosira*) that differ in size but are common phytoplankton species in the area, whereas *Nannochloropsis* and

Tetraselmis are both green flagellate species that are not normally found in this area and were also different sizes.

The results from both the summer and fall experiments, although different, indicate that the composition of a substantial pulse of organic matter did not significantly influence community structure or diversity within the Bonne Bay sedimentary community. No pattern was apparent with respect to treatment from PCA analyses of species composition or community descriptors such as species richness, H' , or abundance.

During different time periods (summer, fall) there appeared to be slight effects of algal composition on infaunal response. ANCOVA analysis revealed that during the summer experiment by week 5 the enrichment treatments combined showed higher expected species shared than controls (Figure 2.1); this pattern was not evident during the fall experiments, which suggests that influence of food supply may only apply to specific periods of the year. Since this is the only analysis to reveal significant difference in biodiversity it is thought that this is a relatively weak response. Evenness also showed an effect, which will be discussed below. What is apparent from the data is the presence of a strong seasonal signal.

Abundance patterns of fauna changed during the sampling period. The first sampling week of the summer experiment had the fewest individuals, whereas the last week of sampling of the fall experiment had the greatest number of individuals (Table 2.1).

Seasonal changes in abundance have been reported in numerous studies (e.g. McCall 1977; Trueblood, et al. 1994; and Kelaher & Levinton 2003) and increases in abundance

have been attributed to the availability of food resources (Kelaher & Levinton 2003) and recruitment events (Renaud et al. 1999) in relation to reproductive strategy (Trueblood et al. 1994). A major recruitment event is probably the reason for the significant increase in abundance in week 5 of the summer experiment; this was the only sampling week where juveniles were abundant (*P. tecta*, and cumaceans, probably *Diastylis* sp.). The cumacean *D. sculpta* has been found to release young in mid-July (Corey 1976); whereas *P. tecta* at slope depths off North Carolina, is thought to recruit year round (Blake 1993), but whether this pattern applies to higher latitudes requires further study. *P. tecta* was found to be an important infaunal predator within the cove (Quijon & Snelgrove 2005) and may have recruited to the cove in response to abundant prey. *P. tecta* growth rates are thought to be rapid and individuals can double their body size in 2 months (Heffernan 1985). At this growth rate, juveniles that recruited in mid-July would be large enough to be identified as adults by mid-September when sampling for the fall experiment occurred, which is presumably why no juveniles were found at that time.

Abundance influences species richness and Margalef's Index which were also significantly higher in week 5 of the summer experiment. Given that samples containing more individuals typically support more species (e.g., Clark & Warwick 2001), it is not surprising that these two abundance-based indices were also significantly higher in week 5. These results are consistent with the seasonal trend in the ambient fauna (Chapter 1).

Evenness, which describes how evenly individuals are distributed among different species, was significantly higher for the *Nannochloropsis* treatments than the *Tetraselmis* treatments during week 1 of the fall experiment ($F_{(3,30)} = 3.05$; $p = 0.032$). For the *Nannochloropsis* treatments, abundance, species richness and Shannon-Weiner diversity were higher, though not significantly, than in *Tetraselmis* treatments. In pollution studies, such as sediment contamination by oil, species are often more evenly distributed compared to uncontaminated sites, which is usually attributable to the decrease in abundance of dominant species and elimination of rare species (Schratzberger et al. 2003). In *Tetraselmis* and *Nannochloropsis* treatments *Astarte* sp., *Crenella* sp., and *P. tecta*, were the most abundant taxa; in each case abundance was at least two times greater in *Tetraselmis* treatments.

One concern with this experimental design is that the treatment could be resuspended and swept away from the artificial patches before any faunal response could occur. Several lines of evidence suggest this was not a problem. The protected nature of the cove results in very little bottom current, and any sediment resuspended by divers was still clearly visible in the water column at the end of the dive 45 minutes later. Digital photographs of cores taken from treatment patches after week 1 of the summer experiment clearly show algal treatments mixed into the sediment to a depth of approx. 1.5 cm. Aside from the photographic evidence, several studies attest to the rapid processing of freshly settled phytodetritus. In a laboratory study involving the polychaete *Nereis diversicolor*, cores treated with ^{14}C labelled *Fucus serratus* exhibited no visible

signs of treatments after just 3 days (Kristensen & Mikkelsen 2003). An *in situ* study off the Carolina margin, using ^{13}C labelled diatoms as the treatment, showed that agglutinated protozoans and surface-deposit feeding polychaetes rapidly consumed the labelled treatment in 1 to 1.5 days (Levin et al., 1999). Many of the species that are numerically dominant in this study, are surface-feeding deposit feeders (e.g. Ampharetidae, Spionidae, and Sabellidae); Paraonid polychaetes are thought to be selective diatom feeders (Fauchald & Jumars 1979), and two genera from this family (*Paradoneis* and *Aricidea*) are well represented in this study (Tables 2.1). With high abundances of surface-feeding deposit feeders, it is likely that any added organic material would have been consumed quickly or mixed deeper into the sediment. Either scenario would have prevented my detection of the enrichments by (1) removing the organic matter from the sediment by ingesting it before I sampled and (2) diluting and burying the treatment below the sediment horizon sampled for CHN (~1 – 1.5 cm).

Fall experiments offer further evidence that treatments were not swept away from patches. Significant differences were observed in C/N ratios from week 1 to week 5, and the lower C/N ratios for week 1 (Figure 2.4) could be indicative of phytodetritus input. Ambient C/N levels declined through the fall, however CHN sampling for week 1 occurred before the trend began (Chapter 1).

Carbon to nitrogen ratios (C/N) provide a general indicator of food quality, and C/N ratios ranged between 5.05 and 19.44 over the duration of all experiments. This range

indicates that food quality ranged from excellent (~ 4) to relatively good (~ 20) (Blackburn et al. 1996; Kendall et al. 1995). Quijon and Snelgrove (2005) reported mean C/N ratios of 15.9 for ambient sedimentary habitats 5 m shallower at the same site and also noted that quality varies substantially from site to site within Bonne Bay. A study by Parrish (1998) in Trinity Bay, Newfoundland found that planktonic lipids passed through the water column virtually unaltered, and were incorporated quickly into the benthic food webs. These values indicate that the sediments around Newfoundland typically contain organic carbon of high quality that would be readily available to the benthic food web, especially during the spring and summer months.

Two other experimental design issues to be considered are the adequacy of patch size and the timing of experiments. Levinton & Kelaher (2004) found that small food-rich patches $\sim 63 \text{ cm}^2$ were colonized at the same frequency as similar-sized, food-poor patches. From these data they suggested that larvae could detect larger patches more predictably; the patch size used in this experiment (998 cm^2) was considerably larger than 63 cm^2 , but was smaller than their suggested patch size (ca. 1 m^2 , Levinton & Kelaher 2004); which would have been impractical using my methods. Smith and Brumsickle (1989) found that patch size influenced colonization; larger patches were colonized predominately by larvae whereas smaller patches were colonized by postlarval stages. They suggested that a patch size between 50 cm^2 and 1750 cm^2 might represent a balance between colonization modes. Visual observations at the Bonne Bay site also supported the suitability of the patch size used in that lobster (*Homarus americanus*)

feeding pits were noted near the transect lines and were similar in size to the experimental patches. In slightly shallower areas adjacent to the sampling site, variably-sized patches of benthic diatoms were observed and high variation in ambient C and N values (Chapter 1) further emphasizes the patchy distribution of organic matter at this site.

Timing of experiments would have been less than optimal had no recruitment events been detected, or had no changes been observed in the ambient community. If no larval recruitment had occurred, then the only means of colonization would have been by post-larval immigration, which would have been difficult to detect given that patches were created over ambient sediment (containing intact communities) on the seafloor. Because juveniles of *P. tecta* polychaetes and cumaceans in particular were abundant at times and were identified as being important by PCA analysis, there was clearly an opportunity for a faunal response to the patches other than adult immigration. Evidence of a strong seasonal signal is evident in algal treatments (e.g. significant changes with time as factor; see Chapter 1). Thus, timing of these experiments was appropriate to capture both potential colonization and immigration; but it is possible that a stronger response might be observed in other taxa at other times of the year.

To provide a more comprehensive understanding of colonization, more natural, *in situ* experiments are essential. The advantages of *in situ* experiments include unaltered sediment geochemistry (Smith and Brumsickle 1989), unaltered bottom flow conditions

(Snelgrove et al. 1992) as well as the realism associated with conducting experiments in the field (Grassle et al. 1980). *In situ* studies with minimal manipulation are less susceptible to methodological biases and artefacts that can be introduced in other cases.

There are disadvantages to using *in situ* experiments. Logistics generally limit such experiments to small scales and low precision (Worm et al. 2000). Predation, which is a major influence in this area (Quijon & Snelgrove 2005) and elsewhere (Schneider, 1978; Schneider 1992; Ambrose 1984), as well as other ecological interactions (Kline & Stekoll 2001) confound any simple interpretation of results. A commonly listed shortcoming of *in situ* enrichment experiments is the lack of measurement of the enrichment (Worm et al. 2000). In the current study, the relatively low frequency of sampling for carbon and nitrogen (e.g. one sampling period for the summer experiment and two sampling periods for the fall experiment) represented a trade-off between the relatively small size of the experimental patch (998 cm²), the logistics of working at 20 m depth, and the desire to minimize disturbance at the site. Unfortunately the fate of the carbon and the time scale involved could therefore not be resolved unambiguously. Newfoundland waters are productive with a seasonal abundance of high-quality food resources (Parrish 1998), as a result this system may be less carbon limited than others and pulses of enrichment represent a weak input relative to ambient availability.

It may be possible that the food sources used were not different enough from each other to elicit different responses. For this experiment 3 different species of phytoplankton

were used as enrichment species to simulate sinking food supply. Although beyond the scope of this study on phytodetritus as a food resource, further work could incorporate more strongly contrasting sources of organic matter (e.g., Snelgrove et al. 1992), such as *Laminaria* sp., or *Fucus* sp., which are abundant within the bay, as an alternative food source; or base the food supply on their respective fatty acid profiles. Nonetheless, it appears that the composition or diversity of a pulsed phytodetrital source does not significantly influence the benthic community dynamics within this ecosystem, at least for the range of organic input types that were tested.

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Table 2.1a: Mean density (individuals 38.5 cm⁻²) and 95% confidence intervals for numerically dominant species for the summer experiment.

Week	Rank	Taxa and densities per treatment									
		T	C	N	M	X					
Wk 1	1	<i>Prionospio steenstrupi</i>	9.5 ± 6.3	<i>Astarte</i> sp.	8.5 ± 3.8	<i>Astarte</i> sp.	7.25 ± 8.4	<i>Astarte</i> sp.	9.5 ± 4.8	<i>Bathymedon</i> sp.	9.5 ± 6.5
	2	<i>Paradoneis lyra</i>	8.5 ± 1.3	<i>Bathymedon</i> sp.	5.25 ± 5.7	<i>Crenella</i> sp.	4.75 ± 5.7	<i>Prionospio steenstrupi</i>	7 ± 2.7	<i>Paradoneis lyra</i>	6.5 ± 3.0
	3	<i>Bathymedon</i> sp.	5 ± 5.5	<i>Crenella</i> sp.	4.75 ± 2.8	<i>Paradoneis lyra</i>	4.25 ± 1.9	<i>Paradoneis lyra</i>	5.75 ± 4.2	<i>Prionospio steenstrupi</i>	4.25 ± 3.2
	4	<i>Astarte</i> sp.	4 ± 3.1	<i>Paradoneis lyra</i>	4.25 ± 2.6	<i>Diastylis lucifera</i>	4 ± 4.2	<i>Aricidea catherinae</i>	4.5 ± 4.7	<i>Astarte</i> sp.	4 ± 1.8
	5	<i>Pholoe tecta</i>	3.5 ± 2.6	<i>Prionospio steenstrupi</i>	4 ± 1.1	<i>Bathymedon</i> sp.	3.5 ± 2.5	<i>Bathymedon</i> sp.	4.25 ± 2.6	<i>Diastylis lucifera</i>	2.25 ± 2.0
		Total	51.5 ± 14.7	Total	47 ± 16.5	Total	45.5 ± 30.7	Total	54.8 ± 20.3	Total	43 ± 13.3
Wk 5	1	<i>Prionospio steenstrupi</i>	9.5 ± 3.3	<i>Astarte</i> sp.	9.25 ± 4.8	<i>Prionospio steenstrupi</i>	12 ± 5.7	<i>Prionospio steenstrupi</i>	10.25 ± 3.5	Cumacean juvenile	34 ± 66.6
	2	<i>Paradoneis lyra</i>	7 ± 4.9	<i>Prionospio steenstrupi</i>	8 ± 5.1	<i>Crenella</i> sp.	5 ± 4.5	<i>Astarte</i> sp.	5 ± 3.8	<i>Pholoe juvenile</i>	11 ± 7.1
	3	<i>Astarte</i> sp.	6.75 ± 5.6	<i>Pholoe juvenile</i>	6.5 ± 6.7	<i>Astarte</i> sp.	4.25 ± 3.2	<i>Pholoe juvenile</i>	4.5 ± 7.6	<i>Prionospio steenstrupi</i>	9.25 ± 4.5
	4	<i>Pholoe juvenile</i>	4 ± 2.1	<i>Crenella</i> sp.	6 ± 2.1	<i>Pholoe juvenile</i>	3.75 ± 3.4	<i>Paradoneis lyra</i>	4.25 ± 2.6	<i>Astarte</i> sp.	7 ± 6.5
	5	<i>Chone duneri</i>	3.25 ± 3.8	<i>Diastylis lucifera</i>	5.25 ± 5	<i>Paradoneis lyra</i>	3.5 ± 2.6	<i>Diastylis lucifera</i>	3.75 ± 7.3	<i>Paradoneis lyra</i>	3.75 ± 0.94
		Total	69 ± 6.5	Total	76 ± 24.8	Total	57.8 ± 23.5	Total	51 ± 27.8	Total	95.5 ± 83.0

Table 2.1b: Fall experiment.

Week	Rank	Taxa and densities per treatment									
		T		Te		N		M		X	
Wk 1	1	<i>Astarte</i> sp.	7 ± 3.2	<i>Pholoe tecta</i>	12.75 ± 6.8	<i>Diastylis lucifera</i>	6.75 ± 4.0	<i>Pholoe tecta</i>	12 ± 9.4	<i>Pholoe tecta</i>	8.5 ± 7.3
	2	<i>Pholoe tecta</i>	6.75 ± 5.7	<i>Diastylis lucifera</i>	11.5 ± 8.4	<i>Astarte</i> sp.	6.25 ± 3.3	<i>Astarte</i> sp.	7.75 ± 11.4	<i>Diastylis lucifera</i>	6.5 ± 3.3
	3	<i>Paradoneis lyra</i>	5.5 ± 2.5	<i>Astarte</i> sp.	10.75 ± 11.9	<i>Prionospio steenstrupi</i>	5.25 ± 3.1	<i>Prionospio steenstrupi</i>	7.25 ± 2.2	<i>Astarte</i> sp.	6.25 ± 5.8
	4	<i>Phyllodoce mucosa</i>	4 ± 2.9	<i>Crenella</i> sp.	7.5 ± 12.1	<i>Crenella</i> sp.	4.75 ± 5.6	<i>Paradoneis lyra</i>	6.5 ± 3.6	<i>Cerastoderma</i> sp.	4.5 ± 5.3
	5	<i>Prionospio steenstrupi</i>	3.75 ± 0.5	<i>Paradoneis lyra</i>	6.25 ± 3.2	<i>Pholoe tecta</i>	4.25 ± 2.8	<i>Crenella</i> sp.	5 ± 5.8	<i>Paradoneis lyra</i>	3.75 ± 0.5
		Total	53.3 ± 6.1	Total	87.8 ± 32.7	Total	61.5 ± 30.8	Total	80.8 ± 30.0	Total	54.3 ± 40.7
Wk 5	1	<i>Astarte</i> sp.	9.75 ± 5.2	<i>Astarte</i> sp.	19 ± 13.8	<i>Astarte</i> sp.	7.5 ± 7.3	<i>Pholoe tecta</i>	13.75 ± 11.9	<i>Paradoneis lyra</i>	5.75 ± 3.8
	2	<i>Pholoe tecta</i>	7.5 ± 6.9	<i>Crenella</i> sp.	15.25 ± 15.7	<i>Crenella</i> sp.	7 ± 7.3	<i>Astarte</i> sp.	9.75 ± 8.3	<i>Pholoe tecta</i>	5.25 ± 3.7
	3	<i>Diastylis lucifera</i>	6.25 ± 1.5	<i>Pholoe tecta</i>	11 ± 6	<i>Pholoe tecta</i>	5.5 ± 6.3	<i>Crenella</i> sp.	5.25 ± 3.5	<i>Astarte</i> sp.	4.75 ± 3.9
	4	<i>Paradoneis lyra</i>	6 ± 2.5	<i>Cerastoderma</i> sp.	5 ± 1.6	<i>Diastylis lucifera</i>	5.25 ± 1.5	<i>Paradoneis lyra</i>	4.75 ± 1.7	<i>Diastylis lucifera</i>	4.5 ± 3.6
	5	<i>Crenella</i> sp.	3.75 ± 2.0	<i>Paradoneis lyra</i>	4.75 ± 3.4	<i>Prionospio steenstrupi</i>	4.5 ± 3.3	<i>Prionospio steenstrupi</i>	4.5 ± 2.5	<i>Cerastoderma</i> sp.	2.75 ± 2.2
		Total	63.8 ± 28.7	Total	103 ± 61.6	Total	54.3 ± 32.3	Total	78.8 ± 35.2	Total	50.5 ± 26.7

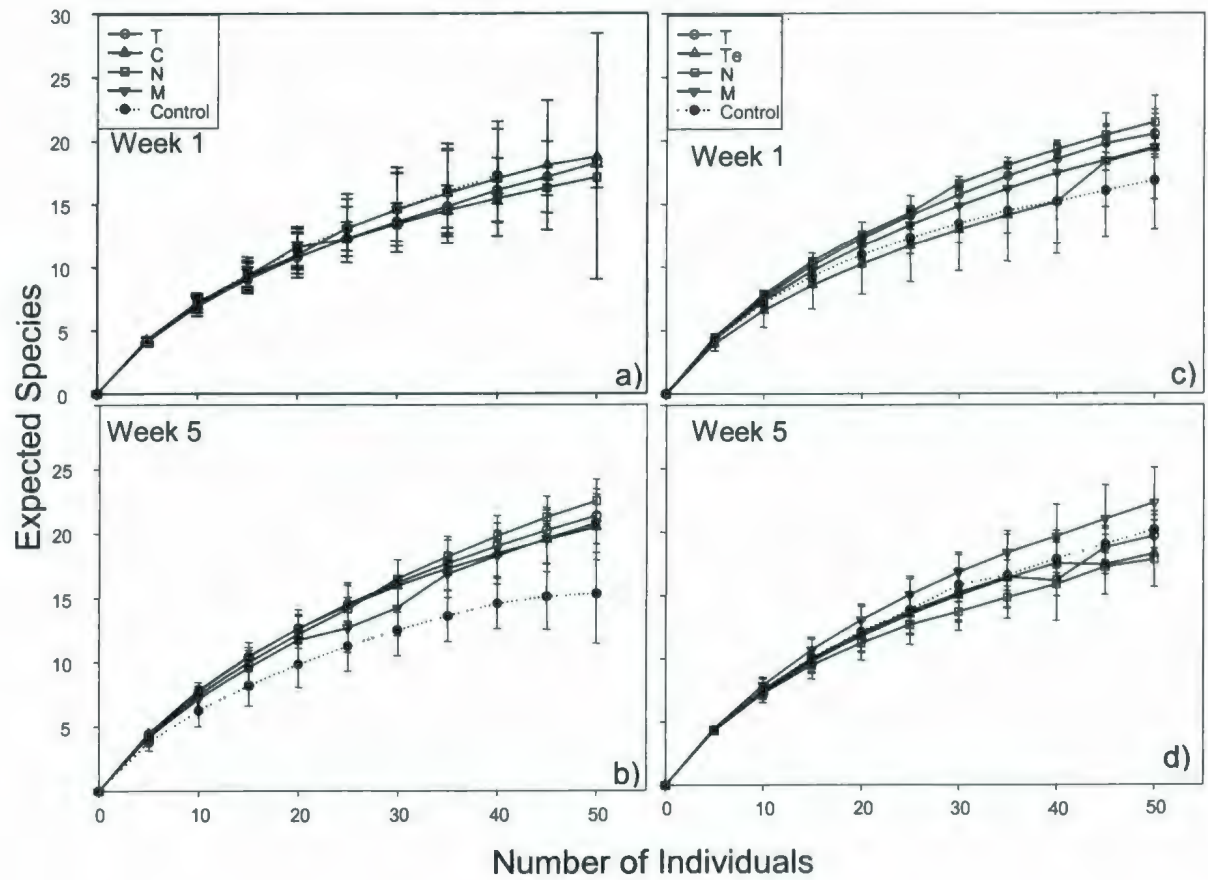


Figure 2.1: Rarefaction curves (means and 95% confidence intervals) for each treatment for the summer experiment, a & b; and the fall experiment, c & d. Treatments; T = *Thalassiosira*, Te = *Tetraselmis*, C = *Chaetoceros*, N = *Nannochloropsis*, M = Mixture, & X = Control.

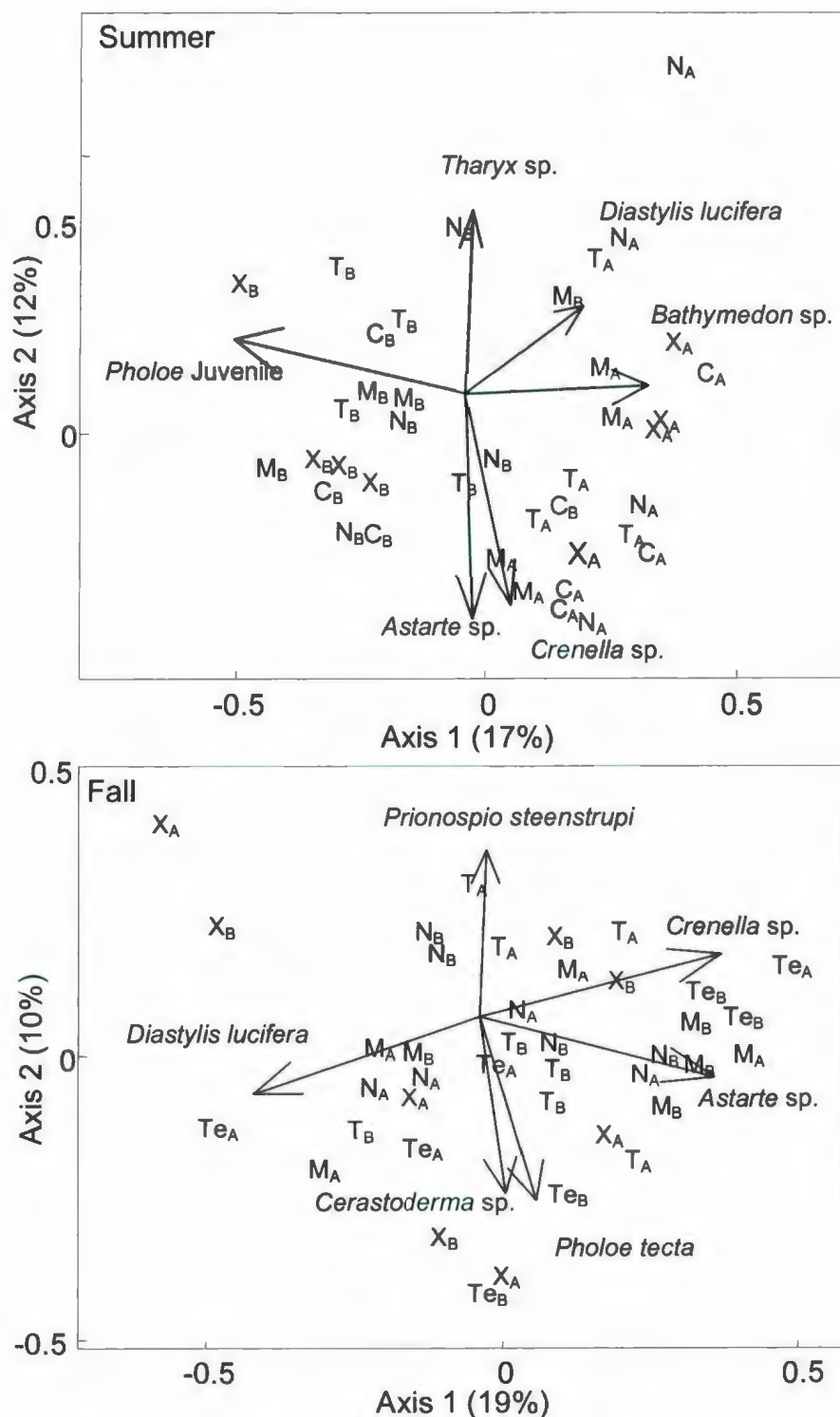


Figure 2.2: Metric scaling of CNESS ($m = 10$) for both weeks of the summer (top) and fall (bottom) experiments. Gabriel Biplot vectors show which species contribute most to pattern. Subscripts denote sampling week (A = Week 1, B = Week 5). For treatment symbols see Figure 2.1.

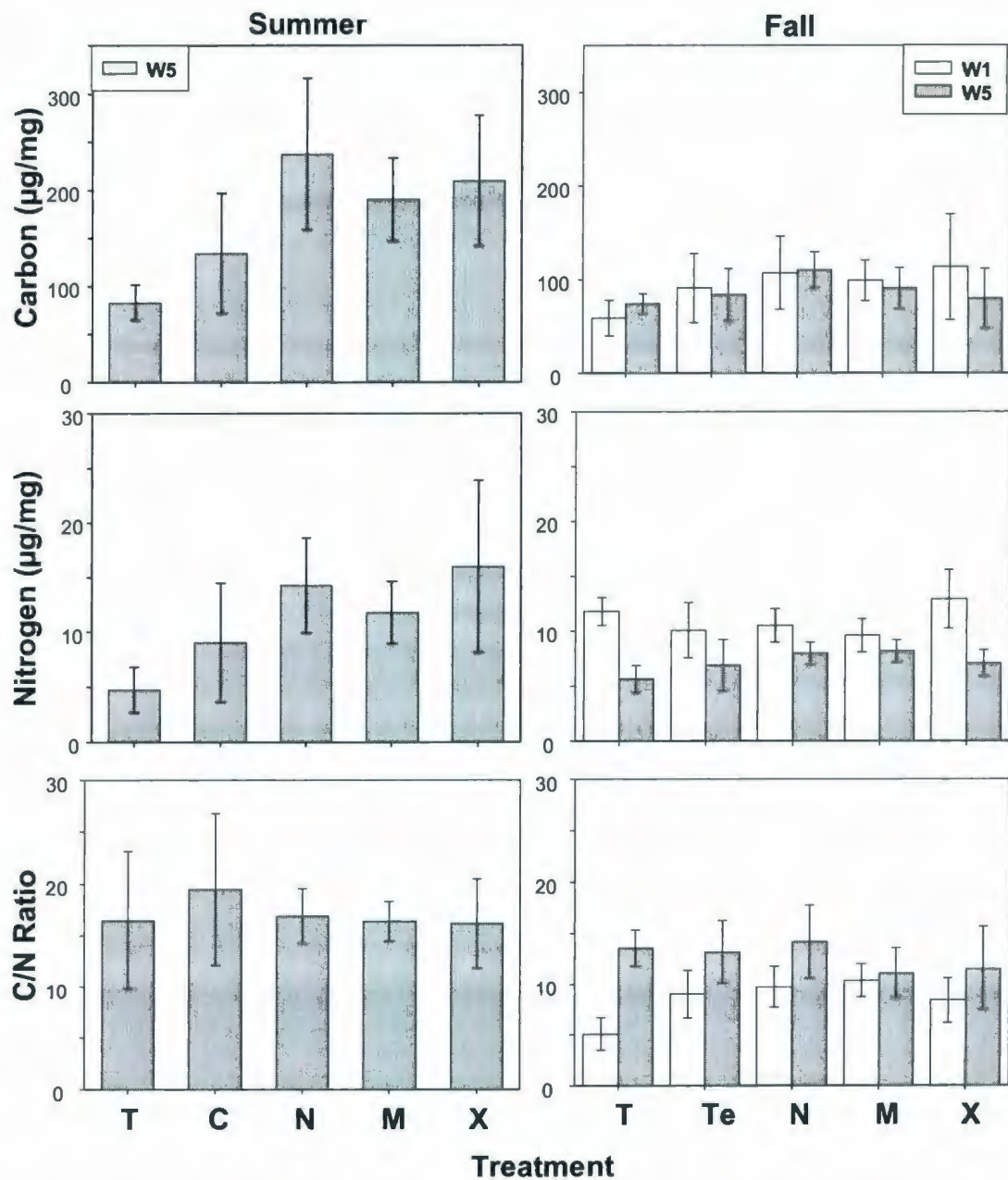


Figure 2.4: Means and 95% confidence intervals for sedimentary carbon, nitrogen and Carbon to Nitrogen (C / N) ratios (by weight) measured in each of the treatments during the experiments conducted in the summer and fall. For the summer experiment data were available for week 5 only. For key to treatments see Figure 2.1

CHAPTER 3

DOES THE QUANTITY OF SINKING PHYTODETRITAL FOOD SUPPLY INFLUENCE SHALLOW-WATER BENTHIC COMMUNITY STRUCTURE?

Data and text from this chapter appears in:

Quijon PA, Kelly MC, Snelgrove PVR (2008) The role of sinking phytodetritus in structuring shallow-water benthic communities. *J Exp Mar Biol.* 366:134-145

3.1 INTRODUCTION

With increased consumption of fossil fuels and subsequent atmospheric emissions of carbon dioxide, the fate of carbon in the global ecosystem has become a major environmental issue (Hopkinson & Vallino, 2005). As much as one hundred million tons of carbon in the form of carbon dioxide is produced by primary production in the worlds oceans each day, and most of this is sequestered into the marine ecosystem by sinking particles (Behrenfeld et al., 2006). As increased amounts of carbon dioxide are absorbed by the ocean the impacts on the functioning of this massive ecosystem are at risk of major changes (Buesseler et al., 2007; Schmittner, 2005).

This sinking production serves as a high quality food source for many oceanic communities, including the benthic sedimentary community (Parrish, 1998; Widbom & Frithsen, 1995). Food supply as a structuring mechanism for benthic communities has been investigated in several studies (Graf, 1987; Josefson & Conley, 1997; Galeron et al., 2000). The significance of food supply as an influence on macrofaunal communities ranges from very important (Grebmeier et al., 1988; Gould & Gallagher, 1990; Stocks & Grassle, 2001), where food could be a limiting resource or have a direct effect on

biomass, to less important, with little or no effect on variables such as polychaete recruitment (Ambrose & Renaud, 1997) or abundance or diversity (Chapter 2).

The organic matter that the benthos receives can have very different effects depending on amounts and timing of delivery (Widbom & Frithsen, 1995; Widdicombe & Austen, 2001). Too much organic matter can have an adverse effect on benthic communities; for example, high organic loads combined with low physical disturbance yielded lower than expected diversity (Widdicombe & Austen, 2001). Numerous eutrophication studies consistently show that high levels of organic enrichment, carbon or other nutrients such as nitrogen or phosphorous generally lead to increases in a few opportunistic species, while decreasing overall diversity and abundance of other less opportunistic species (Oviatt et al. 1986; Widbom & Frithsen, 1995). In more extreme cases, eutrophication can cause such intense oxygen stress that macrofauna can be almost wiped out entirely during warm summer months (Rabalais, 2004); these areas then undergo large recolonization events during the winter (Tagliapietra et al., 1998). Examples of food limitation are rare in shallow temperate areas where the seafloor lies within the photic zone and therefore supports high local primary production (Josefson & Rasmussen, 2000). At the other extreme, deep-sea sedimentary communities are kilometers below the depth of light penetration and generally depend on organic matter sinking down from surface waters. In these cases, studies have shown that community diversity and abundance is often set by food availability and or related disturbances (Grassle & Morse-Porteous, 1987; Snelgrove et al. 1994; Snelgrove & Smith, 2002). The role that sinking

phytodetritus can play in structuring shallow-water communities has been inferred from observation data (see Chapter 1) but experimental studies on the importance of quantity of sinking material are few.

In this experiment I use *in situ* experiments to determine if the quantity of sinking organic matter source (phytodetritus) has an effect on community structure. More specifically, if patches of natural sedimentary communities receive high concentrations of high-quality phytodetritus, will this food resource influence the composition, abundance, or diversity of sedimentary fauna in comparison with similar patches that receive less (i.e. half the level) or effectively no (i.e. ambient control sediment) enrichment?

3.2 MATERIALS AND METHODS

3.2.1 Sampling Site

Experiments were carried out along a 20-m isobath in Small Cove, Bonne Bay NL (Figure 1.1). The artificial patches were oriented along the same two transect lines as the experiments described in Chapter 2 (summer transect line between 49°28.872 N 57°54.551 W and 49°28.837 N 57°54.481 W; fall transect line 49°28.840 N 57°54.485 W and 49°28.798 N 57°54.472 W). For a further description of the sampling site refer to the introduction and overview as well as Chapters 1 and 2.

3.2.2 Establishing Artificial Patches

Artificial patches were created by scuba divers using the same protocol as described in chapter 2, and is described here only briefly. For this experiment, treatments consisted of algal paste (Instant-Algae® from Reed Mariculture) that was consistent in composition among treatments but differed in amount. The treatments were injected with a syringe through a spray bar into the inverted (open bottom) clear plastic (38 cm x 26 cm x 13 cm high) enrichment chamber that had been placed on the seafloor; the spray bar was then flushed with ambient seawater to ensure all of the algae was deployed into the chamber, which was left in place for 24 hours prior to careful removal that minimized sediment disturbance. For controls, ambient seawater only was injected into the chambers but methodologies were otherwise identical.

3.2.3 Experiments

For each experiment (summer and fall) 12 artificial patches were created along a transect line using 3 different treatments of 4 replicates each of low, high, and ambient algal concentration (see below). The composition of the treatment for each set of experiments remained constant, a mixture treatment of 3 algal species consisting of *Thalassiosira weissflogii*, *Chaetoceros gracilis* and *Nannochloropsis*. The treatments for the fall experiment were slightly different from those used in the summer in that the algal species *Tetraselmis* was substituted for *Chaetoceros gracilis*.

The amount of algae added for the high treatment was equivalent to predicted carbon accumulation over a 35 day period (the length of the experiment) at peak spring bloom levels; the low treatment was equivalent to carbon accumulation for 35 days at low mid-summer levels as measured at other coastal sites in Newfoundland: Trinity Bay (Parrish, 1998), Conception Bay (Redden, 1994), and Bonne Bay (Tian et al., 2001). Treatment 3 was an unenriched control treatment which was injected with ambient seawater only. Each patch was sampled as per the sampling regime described in detail in chapter 2, but in brief entailed diver-collected acrylic cores (6.5 cm diameter, 20 cm length) pushed 10 cm into the sediment prior to capping, retrieval, and processing over a 300 μ m sieve. (see Chapter 1). This entire experiment was carried out twice. The first round (summer - 24 cores) was enriched on June 20th, sampled initially on June 30th, and then sampled again on July 26th. The second round (fall – 24 cores) was enriched on August 24th, and then sampled on September 8th and again on October 9th 2002.

Several patches were disturbed before enrichment, in that the chamber was not present when divers returned to apply the enrichment. These patches were prepared again, following the exact same protocol; each patch was sampled within the same time frame as those originally enriched except that they were staggered by one day. For this reason I included the data from these patches with the original patches in a single data analysis.

3.2.4. CHN Sampling

Samples for CHN analysis were taken from each patch using a modified syringe (60 ml syringes with tip removed, see Chapter 1). Samples were taken from each of the replicate patches during the July 26th, September 8th, and October 9th sampling dates for a total of 36 samples. CHN samples were analysed in a CHN analyzer (Perkin-Elmer Model 2400) as outlined in Chapter 1.

3.2.5. Data Analysis

Data from each experiment were analysed separately using both univariate and multivariate methods as described in Chapters 1 and 2. Because environmental conditions in the summer and fall were known to be quite different (see Chapter 1) the two sets of experiments were analyzed separately. CHN samples were analyzed by one- and two-way ANOVAs with treatment or time and treatment as factors, and are presented as plots of means and 95% confidence intervals. For analysis of the macrofaunal data, Primer v5 was used to calculate the univariate measures abundance (N), species richness (S), Margalef's biodiversity index (D), evenness (J), Shannon-Weiner diversity index (H'), and Expected Species Shared based on a sample of 30 individuals (ES[30]). These measures were compared by two-way ANOVA with treatment and time as factors. Plots of means and 95% confidence intervals were also generated for each measure. Assumptions for ANOVA were checked in each case, where assumptions were not met, data was either transformed, or p-values were calculated by randomization.

Hurlbert rarefaction curves (Hurlbert, 1971) were generated using Primer v5; curves were plotted using means and 95% confidence intervals for each treatment for each sampling week. These curves were also analyzed by ANCOVA as described in Chapter 2.

In order to compare community composition, I used the similarity measure CNESS (Chord-Normalized Expected Species Shared, see Chapter 1), based on a random draw of 10 individuals ($m = 10$). As with other analyses, the summer and fall experiments were analyzed separately. All of the samples in a given experiment (i.e. both weeks) were initially included in a single analysis (24 cores), however, there was some indication that time was important and comparisons were subsequently done separately for each sampling week (12 cores) to ensure that any treatment effect was not swamped by temporal differences. Principal Components Analysis (PCA) of the CNESS probability matrix provided a graphical representation of station similarity, over which Gabriel Biplots were overlaid to indicate which species were important in creating the observed patterns. For a further description of CNESS see Chapter 1.

3.3 RESULTS

3.3.1 *Experimental Fauna Overview*

A total of 3300 individuals were collected over the course of the two experiments, including 1489 from 24 cores in the summer experiment and 1811 individuals from 24 cores in the fall experiment. Number of individuals per sampling week ranged from 589 in the summer experiment to 963 in the fall experiment. Total species number was slightly higher in the summer experiment (89 taxa) than in the fall experiment (79 taxa). The broad taxonomic composition of organisms was generally consistent among experiments and sampling weeks, in that polychaetes were always the most abundant group (59-61% of total individuals), with bivalves next (23-25%) and then all other taxa (~16%). The numerically dominant species for each treatment and week of each experiment are shown in Table 3.1.

3.3.2 *Diversity Measures*

Two-way ANOVAs compared abundance (N), species richness (S), evenness (J), Margalef's Index (D), Shannon-Weiner Index (H'), and Expected Species Shared (Es[30]) with treatment (low, high, control), and time (week) and their interaction as factors. For the fall experiment this analysis indicated no significant differences in treatment, time, or their interaction (Table 3.2).

For the summer experiment, abundance was significantly higher in week 5 than in week 1, and there were also significant time by treatment interaction terms for species richness

($F_{(2,18)} = 5.85$; $p = 0.011$) and Margalef's Index (D) ($F_{(2,18)} = 4.95$; $p = 0.019$) showing that these latter variables should be analyzed separately for each week of the experiment. For sampling week 1, analyses indicate that enrichment treatments (low and high) had significantly lower species richness (S) ($F_{(2,9)} = 8.83$; $p = 0.008$) than controls; this is also apparent in rarefaction curves (Figure 3.1 – see below). Results for Margalef's Index (D) were slightly different in that the high enrichment treatment was significantly lower than the control and the low enrichment treatment ($F_{(2,9)} = 5.53$; $p = 0.027$); no significant differences in these variables were detected in week 5 of the summer experiment.

Rarefaction curves plotted for treatment means show that during the summer experiment, after 1 week the high enrichment treatments were somewhat lower in diversity than either the control or the low enrichment treatments; however, this pattern did not persist through week 5 of the experiment. Rarefaction curves for the fall experiment show no notable treatment differences for the first week; however, the high enrichment treatment has slightly lower diversity in week 5 (Figure 3.1). ANCOVA analysis of these curves reveals that these differences were not significant; summer $F_{(5,54)} = 0.300$, $p = 0.911$; fall $F_{(2,48)} = 0.017$, $p = 0.984$.

3.3.3 Multivariate analysis

Principal components analysis (PCA) of the summer experiment generally separated the two sampling weeks along PC1 axis (Figure 3.2). This pattern was driven by several

species, in that polychaetes (*Pectinaria granulata*, *Asebellides lineata*, *Pholoe* juveniles and *Prionospio steenstrupi*) were important in describing samples from week 5, whereas bivalve molluscs (*Crenella* sp. and *Astarte* sp.), amphipods (*Monoculodes* sp.) and other polychaetes (*Paradoneis lyra* and *Pygospio elegans*) were important in describing samples from week 1. Aside from the differences in sampling weeks, enrichment and control samples were intermingled and indicated no discernable pattern. Separate analysis of each week of the experiments showed no pattern for week 1 of the summer experiment, however, by week 5, the low enrichment treatments separated along the PC1 axis, driven largely by adult *Pholoe tecta*; control and high enrichment treatments grouped together with no obvious separation (Figure 3.3b).

PCA for the fall experiment showed no discernable patterns with respect to sampling week although there was some separation of control and enrichment cores (high or low) but no separation of low and high enrichments (Figure 3.2). In separate analysis of each of the weeks of the fall experiment, no pattern was obvious for week 1, however by week 5 three of four control treatments separated from enrichment treatments along both axes, driven primarily by the cumacean *Diastlyis lucifera*. Enrichment treatments 1 and 2 (low and high) tended to group together (Figure 3.3d), with no clear pattern.

3.3.4 Carbon and Nitrogen analysis

Analysis of sedimentary carbon and nitrogen, as well as C/N ratios for week 5 of the summer experiment (no CHN samples were taken for week 1 of the summer experiment)

revealed no significant differences among treatments (Table 3.3; Figure 3.4). For the fall experiment, two-way ANOVA again indicated no significant differences among treatments or between weeks (Table 3.3; Figure 3.4).

3.4 DISCUSSION

Food supply has a variable influence on benthic community structure, however, in temperate northern systems where high-quality phytodetrital food is generally accessible, albeit at varying concentration, food supply can bring a high degree of stability where other biotic factors such as predation (Quijon & Snelgrove, 2005) and abiotic factors such as grain size (McCarthy et al., 2000) also play an important structuring role. Studies from the Bering and Chukchi Seas reported sediment heterogeneity, food supply, and temperature as major regulating factors for benthic community structure (Grebmeier et al., 1989), but the specific role of food supply remains elusive in descriptive studies because other variables often confound interpretation. In these experiments, different quantities of a high quality, diverse food supply appear to play a very minor role in structuring benthic communities at this Bonne Bay location. Indeed, timing appears to play a greater role, even over time scales of weeks. PCA analysis indicated juveniles (*Pholoe* sp. and cumaceans) as important species driving community pattern, this suggests that recruitment events may play an important role in community dynamics. There were significant differences between weeks for abundance and species richness (Table 3.2) as well as sample similarity as shown in PCA analysis for the summer experiment (Figure 3.2), reinforcing the strong seasonal signal shown in both previous chapters. Seasonal signals within macrofaunal communities are widely reported for

temperate latitudes (Dollar et al., 1991; Trueblood et al., 1994; Kelaher & Levinton, 2003; Reiss & Kroncke, 2005), but not at tropical latitudes (McCarthy et al., 2000). In Bonne Bay, organic matter is available for much of the year, but is significantly higher in abundance during and after the spring bloom (Chapter 1).

For the summer experiment, significantly lower species richness (S) and Margalef's Index (D) were observed in enrichment treatments than in controls; for Margalef's Index the high-enrichment treatment was significantly lower than the control and the low enrichment treatment after one week (Table 3.2). In both cases this pattern did not persist until week 5. This pattern suggests that enrichment initially resulted in decreased diversity, but that the effect was relatively short-lived and was not apparent only one month later. This rapid reaction provides further evidence that the response to organic input is quick and easily missed, at least in relatively productive environments where organic matter is abundant (see also Chapter 2). Macrofauna can process fresh detritus at the sediment surface very quickly, on the order of several days (Kristensen & Mikkelsen 2003; Levin et al., 1999). In a mesocosm study, enriched treatments showed a marked increase in a few species that were able to quickly take advantage of fresh phytodetritus and rapidly increased their abundance by fast reproduction and recruitment of juveniles (Widbom & Frithsen, 1995). Although there was no diversity component reported in this mesocosm study, it is likely that a large increase in abundance of a few species will limit the ability of other less opportunistic and reproductively adaptable species to be

successful within the same spatial scale. A similar pattern was not detected for the fall experiment.

Weiking & Kroncke (2005) found that in shallow areas of the North Sea, there were changes in trophic structure within the benthic community depending on the quality and quantity of food supply. Areas with high amounts of organic material were characterized by high abundances of interface feeders and “sand-lickers” such as amphipods. Interface feeders also dominated areas with high amounts of intermediate quality food. Other areas of the bank where food input was variable were inhabited by the highest diversity of feeding types (Weiking & Kroncke, 2005). The feeding strategies of important species during week 1 of the summer experiment included species that were capable of suspension feeding (*Crenella* sp., and *Astarte* sp., Włodarska-Kowalczyk, 2007, *Monoculodes* sp., *P. lyra*, *P. elegans*) or surface deposit feeding (*P. lyra* and *P. elegans*; Fauchald & Jumars, 1979) (Table 3.1 and Figures 3.2 and 3.3). The species that were important in describing samples at week 5 were all polychaetes, and included *P. granulata*, *A. lineata*, *Pholoe* juveniles and *P. steenstrupi* (Table 3.1 and Figures 3.2 and 3.3) that encompassed a broad range of feeding strategies including subsurface deposit feeding (*P. granulata* and *P. steenstrupi*; Whitlatch, 1974; Fauchald & Jumars, 1979) surface deposit feeding (*A. lineata*; Fauchald & Jumars, 1979) and predation (*Pholoe* juveniles; Fauchald & Jumars, 1979; Josefson, 1987; Quijon & Snelgrove, 2005). This pattern suggests that the species that were best able to respond rapidly to phytodetritus input, namely surface deposit feeders and suspension feeders, were present within a

week of delivery of the enrichment. After the pulse of enrichment was processed, either consumed directly or worked deeper into the sediment, a broader range of feeding strategies (sub-surface deposit feeders, surface deposit feeders and predators) was most important in driving community pattern.

Results show high levels of variance in almost all variables measured, which is consistent with previous studies of shallow water benthic communities (e.g. McCall, 1977). This variance can make detection of any weak effects, and thus interpretation of results, difficult particularly given that the highest levels of abundance in the ambient community and the highest variances occurred in the fall during the sampling periods for the fall experiment (see Chapter 1). One approach to reducing experimental variance is to increase the number of samples (e.g. increasing the number of replicates per treatment: Bartlett et al., 2001), which is impractical in this intensive field experiment because of the limited bottom time available to divers at this working depth.

Although the enrichments in this experiment were not detected in measurements of carbon and nitrogen taken during the summer or fall experiment (Figure 3.4), there are several lines of evidence that phytodetritus persisted at the field site beyond the initial deployment (i.e. it was not resuspended). As discussed in Chapter 2, the phytodetritus was still visible in some replicates after the first week. Moreover, the significant changes observed in species richness and diversity in enrichments suggests it persisted long enough for organisms to respond. That phytodetritus was either quickly consumed or

worked deeper into the sediment beyond the sampling depth is substantiated by the observation of significant effects (species richness, diversity, abundance) after one week but no detectable response after 5 weeks (Table 3.2). These results point to a dynamic benthic fauna, capable of reacting to disturbances on a very short time scale.

These experiments show that the amount of food reaching the benthic community in this study site had a very modest effect on structuring the abundance or diversity of the sedimentary fauna. While some significant results with respect to diversity measures in the first week of the summer experiment indicate that a pulse of food may initially decrease diversity (Table 3.2), this reaction is short-lived, lasting from days to a few weeks. In boreal, highly productive, shallow-water sites, food availability may not be particularly limiting, and the quantity of sinking food supply may therefore play a very minor role in structuring benthic abundance or diversity.

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Table 3.1: Mean densities (individuals•38.5⁻²) and 95% confidence intervals for the five numerically dominant species.

Season	Week	Rank	Taxa and densities per treatment					
			Low		High		Control	
Summer	Wk 1	1	<i>Paradoneis lyra</i>	7.25 ± 5.3	<i>Astarte</i> sp.	7.75 ± 5.6	<i>Astarte</i> sp.	12.25 ± 10.2
		2	<i>Astarte</i> sp.	4.25 ± 3.0	<i>Paradoneis lyra</i>	5.5 ± 4.1	<i>Crenella Monoculodes</i> sp.	5.5 ± 5.6
		3	<i>Prionospio steenstrupi</i>	2.50 ± 1.7	<i>Crenella</i> sp.	3.5 ± 3.4	<i>Prionospio steenstrupi</i>	5 ± 4.5
		4	<i>Cerastoderma</i> sp.	2.25 ± 2.0	<i>Monoculodes</i> sp.	2.25 ± 3.2	<i>Paradoneis lyra</i>	4 ± 2.8
		5	<i>Monoculodes</i> sp.	1.75 ± 1.2	<i>Prionospio steenstrupi</i>	2 ± 1.8	<i>Tharyx</i> sp. <i>D. lucifera</i>	2.5 ± 1.3
		Total		37.5 ± 5.21	Total	40.5 ± 13.4	Total	69.25 ± 26.4
	Wk 5	1	<i>Prionospio steenstrupi</i>	9.5 ± 6.1	<i>Cumacean</i> juvenile	23.25 ± 45.6	<i>Prionospio steenstrupi</i>	12.5 ± 5.2
		2	<i>Paradoneis lyra</i>	6.25 ± 1.5	<i>Prionospio steenstrupi</i>	7 ± 4.2	<i>Astarte</i> sp.	7.5 ± 10.2
		3	<i>Pholoe tecta</i>	4.5 ± 3.6	<i>Astarte</i> sp.	5.75 ± 3.7	<i>Pholoe</i> juvenile	7 ± 2.4
		4	<i>Astarte</i> sp.	4.25 ± 2.8	<i>Pholoe</i> juvenile	5 ± 2.5	<i>Crenella</i>	4.5 ± 5.1
		5	<i>Asebellides lineata</i>	3.25 ± 1.7	<i>Paradoneis lyra</i>	4.75 ± 3.3	<i>Paradoneis lyra</i>	4.25 ± 3.5
		Total		60.5 ± 9.8	Total	91.25 ± 48.6	Total	73.25 ± 31.2
Fall	Wk 1	1	<i>Pholoe tecta</i>	14.25 ± 5.9	<i>Pholoe tecta</i>	12.5 ± 4.3	<i>Diastylis lucifera</i>	14.5 ± 7.7
		2	<i>Astarte</i> sp.	10.5 ± 5.7	<i>Astarte</i> sp.	11.5 ± 6.0	<i>Astarte</i> sp.	9.5 ± 7.1
		3	<i>Diastylis lucifera</i>	8.75 ± 6.4	<i>Prionospio steenstrupi</i>	9.0 ± 9.4	<i>Pholoe tecta</i>	6.5 ± 6.2
		4	<i>Paradoneis lyra</i>	6.5 ± 1.9	<i>Diastylis lucifera</i>	7.5 ± 1.3	<i>Cerastoderma</i> sp.	4.75 ± 0.9
		5	<i>Cerastoderma</i> sp.	6 ± 2.3	<i>Crenella</i> sp.	7.25 ± 5.3	<i>Prionospio steenstrupi</i>	4.5 ± 2.3
		Total		84 ± 18.6	Total	85 ± 30.9	Total	71 ± 8.6
	Wk 5	1	<i>Pholoe tecta</i>	17.25 ± 10.0	<i>Pholoe tecta</i>	12.5 ± 8.5	<i>Diastylis lucifera</i>	9.5 ± 3.7
		2	<i>Astarte</i> sp.	7.75 ± 2.8	<i>Astarte</i> sp.	10.5 ± 5.1	<i>Pholoe tecta</i>	5.0 ± 3.9
		3	<i>Cerastoderma</i> sp.	5.75 ± 1.5	<i>Prionospio steenstrupi</i>	8.25 ± 2.9	<i>Chone dumeri</i>	4.75 ± 2.44
		4	<i>Paradoneis lyra</i>	5.25 ± 1.2; ±	<i>Paradoneis lyra</i>	6.75 ± 3.7	<i>Prionospio steenstrupi</i>	4.25 ± 0.5
		5	<i>Diastylis lucifera</i>	4.75 ± 2.4	<i>Crenella</i> sp.	5.75 ± 6.7	<i>Paradoneis lyra</i> ; <i>Astarte</i> sp.	3.75 ± 2.2; ±
		Total		79.25 ± 14.5	Total	78 ± 28.9	Total	54.75 ± 9.3

Table 3.2: Results of two-way ANOVA comparisons of diversity measures for the Summer and Fall experiments.

Season	Dependent variable	ANOVA's sources of variation					
		Treatment		Week		Interaction	
		F _(2,18)	P	F _(1,18)	P	F _(2,18)	P
Summer	S	1.711	0.209	7.795	0.012	5.853	0.011
	N	1.434*	0.252	5.359*	0.032	1.470*	0.262
	D	0.903	0.423	3.016	0.100	4.948	0.019
	J	0.849*	0.051	0.881*	0.416	0.185*	0.878
	H'	1.094	0.356	0.439	0.516	1.229	0.316
	ES(30)	0.860	0.441	0.005	0.945	1.244	0.313
Fall	S	2.062	0.156	0.256	0.619	0.256	0.777
	N	2.182*	0.162	1.265*	0.270	0.156*	0.842
	D	1.598	0.230	0.025	0.877	0.735	0.494
	J	0.102	0.904	1.303	0.269	1.258	0.308
	H'	1.083	0.360	0.101	0.755	1.533	0.243
	ES(30)	0.680	0.519	0.714	0.409	3.016	0.074

* P-values were calculated from randomly generated F-values with 500 iterations.

Table 3.3: Results of one-way (Summer) and two-way (Fall) ANOVA comparisons of Carbon, Nitrogen, and C/N ratios. NA: Not applicable.

Season	Dependent variable	ANOVA's sources of variation					
		Treatment		Week		Interaction	
		$F_{(2,8)}$	P	$F_{(1,18)}$	P	$F_{(2,18)}$	P
Summer	C	0.602	0.571	NA	NA	NA	NA
	N	0.178	0.840	NA	NA	NA	NA
	C/N	0.387*	0.402	NA	NA	NA	NA
Fall	C	0.467*	0.634	0.052*	0.808	0.219*	0.836
	N	2.189*	0.164	3.278*	0.080	0.076*	0.946
	C/N	0.136	0.874	2.300	0.147	0.174	0.842

* P-values were calculated from randomly generated F-values with 500 iterations.

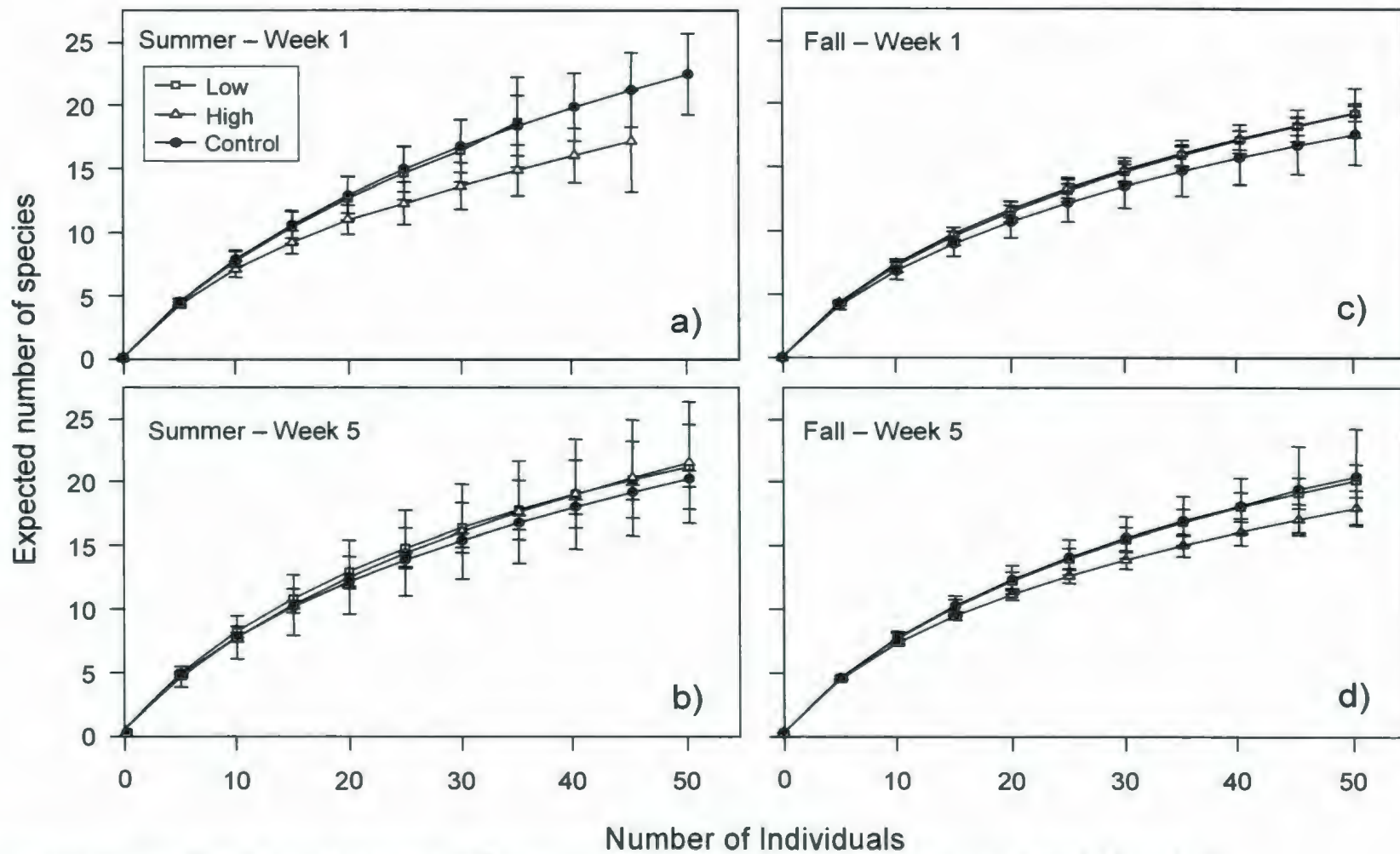


Figure 3.1: Mean Rarefaction curves and 95% confidence intervals for the summer (a & b) and fall (c & d) experiments.

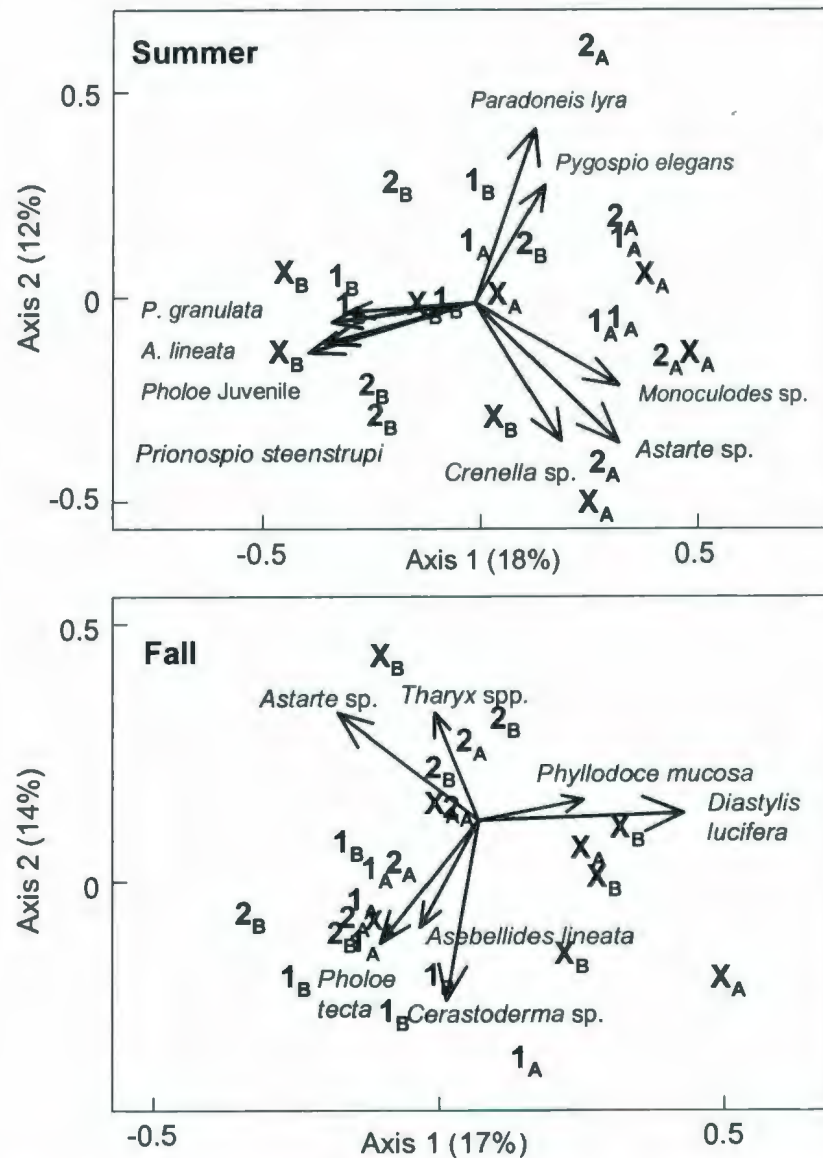


Figure 3.2: Metric scaling of CNESS ($m = 10$) for both the weeks of the summer (top) and fall (bottom) experiments. Gabriel Biplot vectors show which species contribute most to the community patterns. Subscripts denote sampling week (A = week; B = week 5). Treatments: 1 = Low; 2 = High; X = Control).

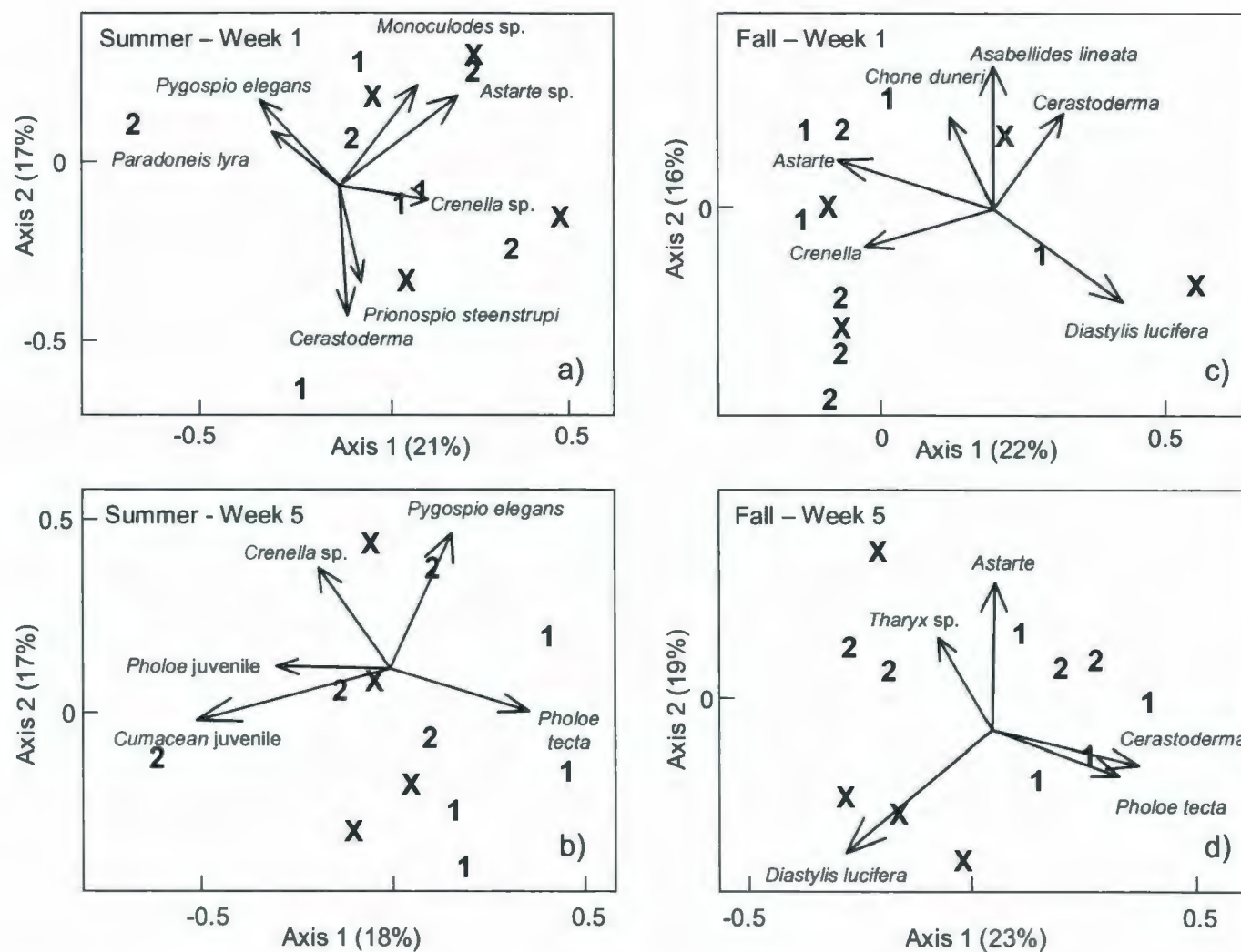


Figure 3.3: Metric scaling of CNESS ($m = 10$) for the summer experiment (a & b) and the fall experiment (c & d). Gabriel biplot vectors show which species contribute most to the community pattern. Treatments: 1 = Low; 2 = High & X = Control.

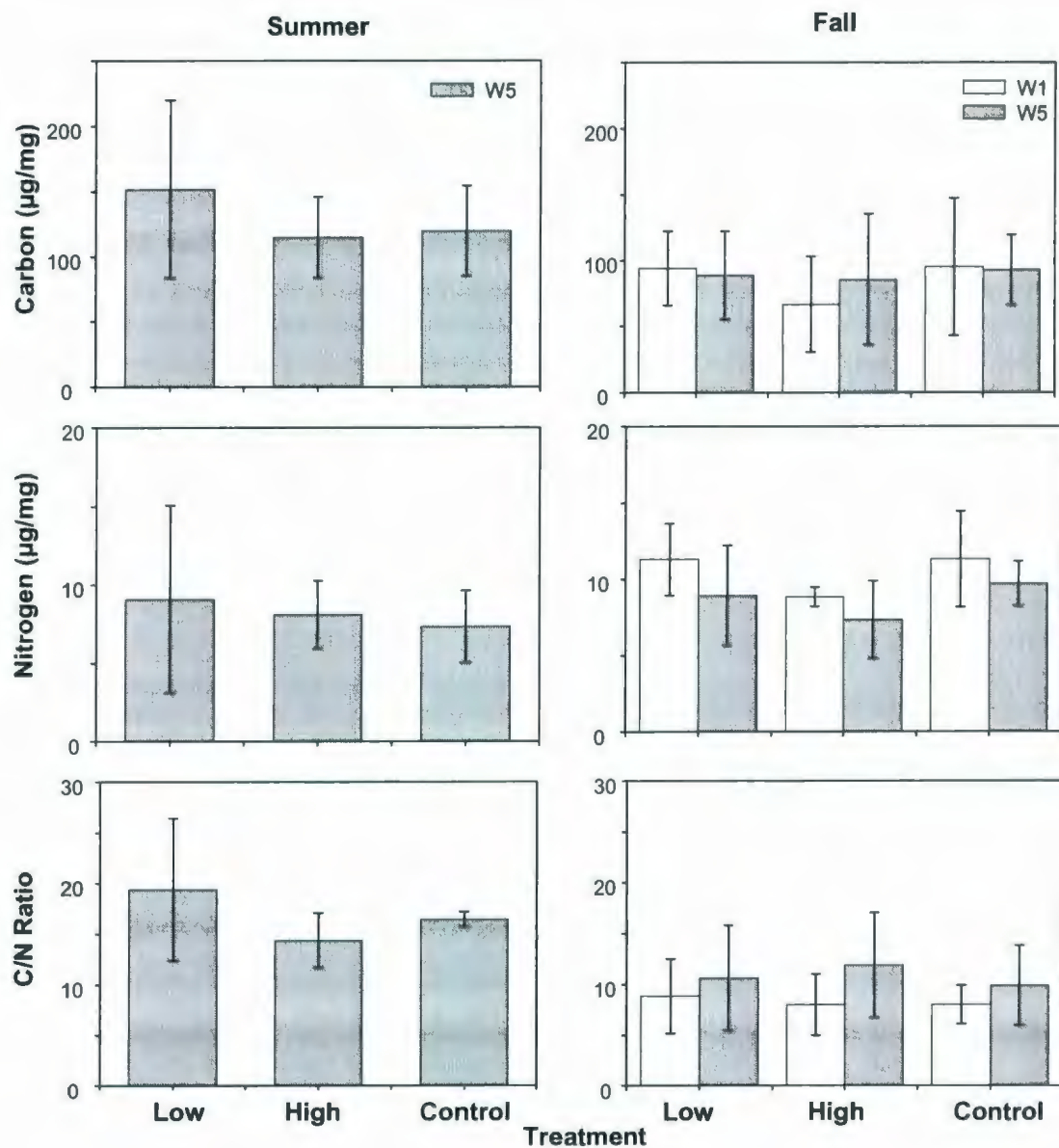


Figure 3.4: Means and 95% confidence intervals of sedimentary carbon and nitrogen as C/N ratios measured in each of the treatments during the experiments conducted in the summer and fall. For the summer experiment data were available for week 5 only.

CHAPTER 4

SUMMARY AND GENERAL CONCLUSIONS

This thesis encompassed three elements that are either new to this type of investigation, or represent an underutilized approach. The first of these elements was the *in situ* experimental approach to address responses to food inputs (Quijon et al., 2008).

Although several studies have manipulated fresh, natural sites to investigate sedimentary biodiversity, most have involved mesocosm, flume, or laboratory manipulations (Oviatt et al., 1984; Smith & Brumsickle, 1989; Snelgrove et al., 1992; Widbom & Frithsen, 1995; Stocks & Grassle, 2001; Widdicombe & Austen, 2001). Studies that take place directly on the sea floor in the same capacity as this work are less common, in large part because the logistical challenges are significant, requiring divers or submersibles. This approach offers a far more natural experimental approach to understanding biodiversity patterns in sedimentary communities because the degree of disturbance to the community is minimized and the environment is as realistic as possible. The same realism that makes such an approach more appealing also creates problems in that the environment cannot be controlled and is more variable than in controlled laboratory experiments. A second novel element was experimental manipulation of food supply. Although food supply is crucial to all sedimentary communities, and is certainly considered to be one of the main factors that influences sedimentary biodiversity patterns (e.g. Grassle & Morse-Porteous, 1987; Graf, 1989; Snelgrove et al., 1992), quality and quantity of food supply is relatively poorly studied for shallow water sedimentary communities (Quijon et al., 2008 and references therein). The other novel element of this

work is the enrichment approach itself. To date, addition of fresh phytodetritus to natural sediments has been rarely used (though see Levin et al. 1999 for a deep-sea application). My findings indicate that this method of enrichment can be completed reliably (i.e. there are visible signs of phytodetritus persistence and mixing in the sediment column up to ~ 1.5 cm) and with minimal disturbance to the resident infauna. This approach opens up an array of potential possibilities for future research.

The sections below further discuss this approach, the findings of this work, and address important questions related to food supply and its role in structuring benthic communities. As a final part of this chapter, I propose a few further potential research directions derived from the studies conducted for this thesis.

4.1 Seasonal variation

Chapter 1 explored natural variation in sedimentary fauna, phytoplankton and pigment concentrations, as well as sedimentary carbon and nitrogen levels from May to October, 2002 in a small cove in Bonne Bay, Newfoundland. Samples were collected at roughly two-week intervals during the sampling period to provide a context and control samples for the experimental chapters that followed. By collecting data from the ambient community, I was able to evaluate natural community dynamics in the absence of manipulation, and to understand changes in the fauna within experimental manipulations but in the context of ambient community dynamics.

Analysis of chlorophyll and phaeopigments in the water column showed high pigment levels both in surface and near-bottom waters in May which then decreased through July before spiking in August and declining to the lowest observed levels in October coinciding with the shortest day lengths of the observation period. Qualitative observations of the phytoplankton community showed strong fluctuations in abundance and composition of phytoplankton through the course of the study period. Sediment pigment analysis indicated that a pulse of phytodetritus reached the sediment between the May sampling dates, and sedimentary phaeopigments were a significant predictor of macrofaunal abundance. Thus, macrofaunal abundance was strongly seasonal in that total abundance increased significantly over time and with “season” as a factor. Several types of multivariate analyses, as well as CHN data, suggested that sampling encompassed four periods that included a May group (two May sampling dates), a June group (three sampling dates), a July group (one sampling date) and a fall group (three sampling dates from August to October). The sharpest increase in abundance occurred between the June and July periods when abundance more than doubled, suggesting that recruitment around that time was quite high. One of the key species during the fall period was the polychaete *Pholoe tecta*, which is a predatory species that may have been recruited to the cove in response to increased abundances of prey species. This recruitment event might also underline the importance of recruitment events in this study area and how they might contribute to community pattern. The data from this chapter show a very strong seasonality of macrofauna abundance within the cove from May to October; it also suggests that abundance and diversity of macrofauna peak when food

levels are relatively low, likely reflecting a short lag between increased food supply and recruitment.

4.2 The contribution of food composition and diversity to biodiversity patterns

Chapter 2 reports on the first of two related but separate experiments. In this chapter I hypothesized that composition and diversity of sinking phytodetritus would influence macrofaunal pattern specifically, do different types of phytodetritus attract different colonizers or groups of colonizers? Does a diverse food source attract a more diverse fauna, or higher abundance of different species than a more homogeneous food source? To test this hypothesis I conducted *in situ* manipulative experiments in Bonne Bay where I deposited fresh phytodetritus to the natural sedimentary sea floor at 20 m depth, but where patches varied in composition and diversity. As characterized in Chapter 1, a strong seasonal signal was also evident in the macrofaunal community in experimental patches. Abundance was significantly higher in week 5 of the summer experiment compared to week 1, and multivariate analysis also indicated differences in faunal composition. There was also evidence of a strong recruitment event between weeks 1 and 5 of the summer experiment juveniles, where the polychaete *P. tecta* and the cumacean *Diastylis* sp. were numerically dominant. This recruitment event was primarily responsible for the significant difference in abundance, and may likely have contributed to differences in species richness and Margalef's Index between week 1 and week 5 of the summer experiment. Despite these dynamic "background" events, the composition of the phytodetrital food pulses tested had little effect on macrofaunal

community diversity, structure, or species composition at this site. There was an increase in Hurlburt diversity (ES[30]) in enrichment versus non-enrichment treatments in the summer experiment over 5 weeks, but the effect was modest and was unrelated to phytodetrital composition. Newfoundland waters are highly productive, and shallow-water Bonne Bay macrofaunal communities may be less food limited than many other benthic environments. Indeed, it has been suggested that alteration of systems like coastal Newfoundland through large-scale removal of pelagic and demersal fishes has resulted in increased energy flow to the benthos (Worm and Myers, 2003). Large pulses of phytodetritus may therefore have little effect on community diversity and structure. Composition of phytodetritus did not influence sedimentary community response, although it is possible that other sources of organic material could play a role in habitat partitioning. This possibility represents an avenue for future research.

4.3 The quantity of food supply as a contributor to biodiversity patterns

Chapter 3 addressed the importance of quantity of sinking phytodetritus from surface waters, which is thought to represent a prime source of high quality food supply for marine benthic organisms. *In situ* enriched patches were created using the same protocols as used for the experiments in Chapter 2 with high and low levels of phytodetrital enrichment. After one week and five weeks, macrofauna in the patches were sampled and compared with ambient sediments where no phytodetritus had been added. The experiment was conducted during the summer and then repeated in the fall in order to evaluate how seasonal variation in available colonizers might influence infaunal

response. Despite significant temporal changes in macrofaunal abundance and composition within and between experiments, the only response that could be attributed to the phytodetritus addition was a rapid response during the first week of the summer experiment. Multiple measures of diversity (species richness, rarefaction, Margalef's index) indicated reduced diversity with phytodetritus addition, but these responses did not persist through the five weeks of the summer experiment and were not observed at all during the fall experiment. These results suggest that the effect of food supply is short term and strongly dependent on seasonal timing. In both experiments, the organic material was largely undetectable even after one week. The rapid utilization of phytodetrital patches in shallow-water environments, in concert with higher background levels of phytodetrital flux, may represent a key difference in structuring of shallow-water and deep-sea sedimentary communities. Experiments in deep-sea environments have indicated much clearer and persistent effects (see Snelgrove and Smith, 2002)

4.4 Further analyses and suggestions for further research

Several parallel analyses were conducted along with those reported in Chapters 1-3. The data analyzed and the results and implications are discussed below.

Analysis of abundance between preserved fractions, several deep fractions (5 – 10 cm) of randomly chosen sediment cores were picked and enumerated. These fractions showed significantly lower abundance and in terms of contributing to community pattern was deemed unimportant, this decision saved countless hours of sample processing.

Nonetheless, one avenue that could be further explored for experimental sediment is the vertical distribution of organisms within the sediment. It is possible that if bioturbators quickly bury fresh phytodetritus (Widdicombe et al., 2000) this could affect the vertical distribution of species, as different feeding guilds react to the input of detritus. Given the major declines in abundance noted here between the 0-5 cm and 5-10 cm fractions, such an analysis would likely need to focus on subdivisions of the upper sediment layers (e.g., 0-1 cm, 1-2 cm etc.)

Body size analysis for *Prionospio steenstrupi*, a numerically dominant species seen in virtually all samples, was carried out for several cores from chapter 1 and chapter 2 data. Total body length was measured and frequency distributions were plotted. No trends could be found relating body size to treatment or to sampling date. This analysis did reveal that small worms (< 5 mm) were much more abundant than larger worms (> 5 mm), and that there was a large amount of variation in body size within each data set. Because this analysis did not reveal any trends in body size in relation to treatment, these data were not repeated for Chapter 3. Nonetheless, further analyses could consider other taxa in order to investigate body size differences in other species and to test for community-level differences. In such an analysis care should be taken to choose species that are well represented across all treatments. Species that are identified by multivariate analysis as important contributors to pattern and that are well represented across the treatments would be the ideal candidates.

Post-hoc power analysis was carried out for several experiments to calculate the necessary sample size to detect significant differences in several of the univariate measures. In most cases, power analysis indicated the need for greater numbers of samples in order to detect significant changes within the population because the data were so variable. Nonetheless, several authors have argued that post-hoc power analysis is fundamentally flawed and should not be used (Lewis, 2006; Steidl & Thomas, 2001). Moreover, additional macrofaunal samples were not obtainable within these protocols because of the size of the experimental patches; any more than 2 sediment cores per patch (1 for week 1, and 1 for week 5) would have completely obliterated the patch. Enlarging the patches would have been very complicated given the logistics of diver working time limitations at 20 m depth. Based on the high variances reported for nearly every measure in this experiment, the “ideal” number of samples indicated by power analysis, would have been very large and therefore logistically impossible to achieve. Given the need for large numbers of samples in order to detect an effect, it is clear that any possible effect of phytodetrital enrichment is not strong and raises the question of whether such an effect would be ecologically important at the spatial and temporal scales studied here.

An analysis of feeding guilds was carried out for each experiment. Nine different feeding guilds were identified from the experimental species including; surface deposit feeders, general deposit feeders, carnivores/predators, subsurface deposit feeders, non-selective deposit feeders, selective deposit feeders, filter feeders, herbivores, and suspension

feeders. For each of the four experiments the samples were analyzed using ANOVA to test for differences in abundances of different feeding guilds with week and treatment as factors.

For every experiment, surface deposit feeders numerically dominated the fauna ranging from 26 - 35% of the total abundance, while carnivores/predators were always next ranging between 18 – 24% of the total abundance. In terms of numbers, the other feeding guilds did not show any consistent pattern, and were scattered in their ranking. Although the result is not significant, the abundance of filter feeders (namely *Astarte* sp.) were consistently higher during the fall experiments as opposed to the summer experiments, since *Astarte* sp. is thought to be a relatively long-lived species (to 20 years) and slow-growing (Trutschler & Samtleben, 1988) it is unlikely they are new recruits that responded to the experimental enrichments.

For the summer experiment of Chapter 2 (quality and diversity experiments) there were several significant results. Surface deposit feeders were significantly higher during week 5 of the experiment compared to week 1 ($F_{(1,30)} = 6.34$); as surface deposit feeders were the dominant feeding group for the entire sampling period, it follows that their numbers would increase significantly during the same period as the ambient fauna significantly increased (Table 1.4; Figure 1.5). The only significant result with treatment as a factor were the general deposit feeders ($F_{(4,27)} = 5.71$). This result is anomalous, general deposit feeders were relatively few in number during this study, numbering only 240 individuals.

The result is significant because of a recruitment event involving juvenile cumaceans. A single sample from the week 5 control samples contained 137 individual juvenile cumaceans, accounting for over half of the total general deposit feeders for the entire experiment.

The summer experiment of Chapter 3 (quantity experiments) had significant results for surface deposit feeders ($F_{(1,17)} = 18.78$); carnivores/predators ($F_{(1,17)} = 10.22$) and selective deposit feeders ($F_{(1,17)} = 7.86$) with week as factor; no results were significant with treatment as factor. Total abundance for the summer experiment of chapter 3 was significantly higher during week 5 (Table 3.2); this significant increase in abundance explains the significant results for both surface deposit feeders as well as carnivores, which together made up 53% of the total individuals for the entire experiment. Selective deposit feeders showed a four-fold increase in abundance between week 1 and week 5 which was mostly attributed to the polychaete *Pectinaria gracilis* and *Pectinaria* juveniles. *P. gracilis* was only represented by a single individual during week 1 of the experiment, while several juvenile individuals were counted; during week 5, the number of *P. gracilis* was 35 and no juveniles were observed. Pectinariids are selective deposit feeders that feed below the sediment water interface in the head down position (Fauchald & Jumars, 1979). Members of the genus *Pectinaria* are known to be highly selective in their feeding practices (Whitlatch, 1974), and it is possible that these polychaetes are feeding on organic matter which had been buried by bioturbators. Because there was no

significant effect with treatment as factor it is not possible to comment on whether these worms are feeding on the experimental additions.

For both fall experiments (chapter 2 – quality and diversity and chapter 3 – quantity) there were no significant differences between feeding guilds for either factor; treatment or week.

The results of the feeding guild analysis support the general conclusion that food supply to the macrofaunal community at this study site had relatively little structuring effect on the community at the temporal and spatial scales that were tested.

In studies that focus on community dynamics, often the biology of individual species is necessarily overlooked. In a study that contains hundreds of species, it is impossible to fully evaluate the biology of each individual species. This thesis consistently identified several species that made important contributions to community patterns. In future studies it may be worthwhile to identify which species make such contributions and study them in a controlled laboratory setting to further understand their individual biology, ecology, and nutrition on a much reduced scale.

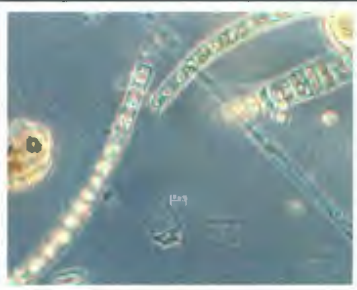
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- Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84: 162-173

Appendix A

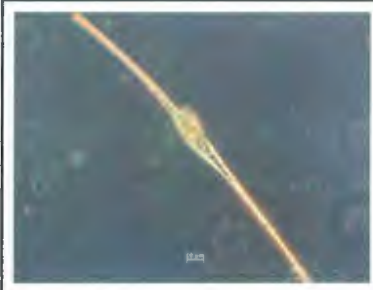
Micrographs of representative phytoplankton species. Size bars are 10 μm except for *Ceratium longipes*, *Chaetoceros contortus*, *Chaetoceros debilis*, *Dinobryon belagacea* & *D. balticum*, *Dinophysis roundata*, *Dinophysis norvegica*, *Protoperidinium depressum*, and *Thalassiosira anguste-linea* where the bar is 20 μm .



Bacterosira bathyomphala



Ceratium arcticum



Ceratium fuscus



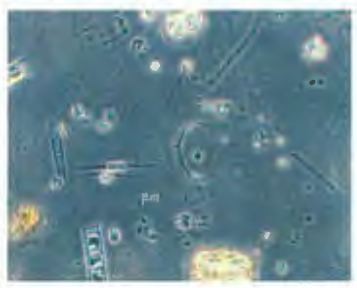
Ceratium longipes



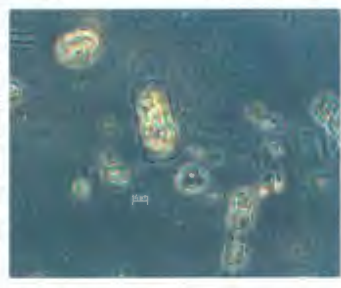
Chaetoceros contortus



Chaetoceros debilis



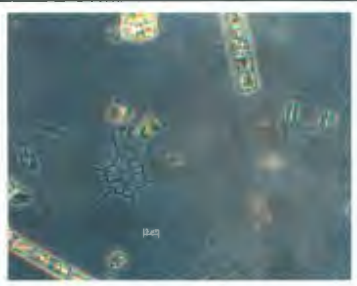
Cylindrotheca closterium



Dactyliosolen fragilissimus



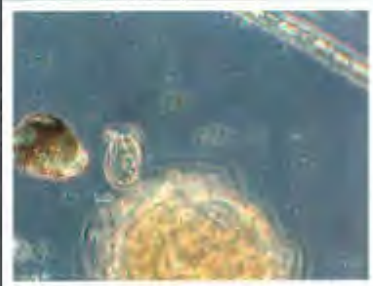
Detonula confervacea



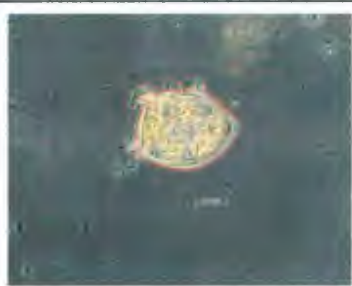
Dictyocha speculum



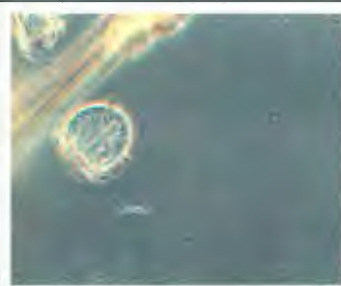
Dinobryon belgacea & *D. balticum* (longer)



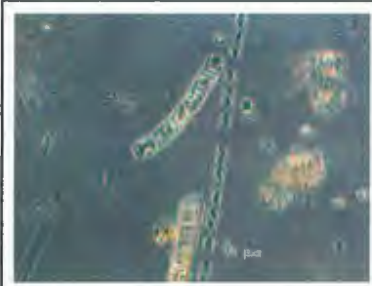
Dinophysis cf *acuminata*



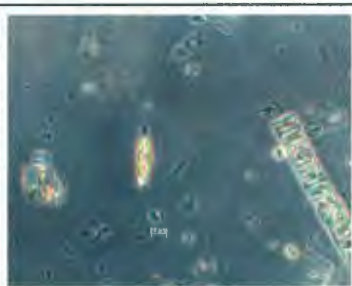
Dinophysis norvegica



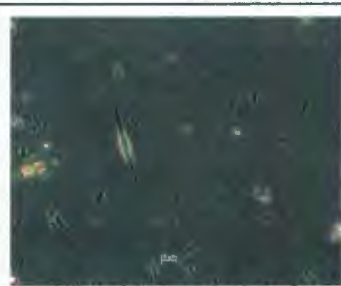
Dinophysis rotundata



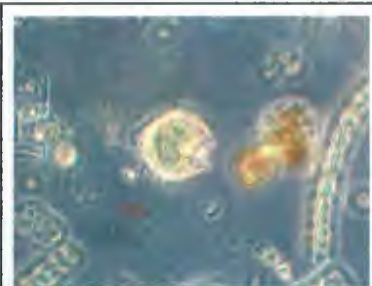
Leptocylindrus danicus



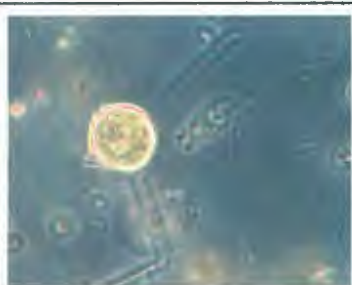
Navicula sp.



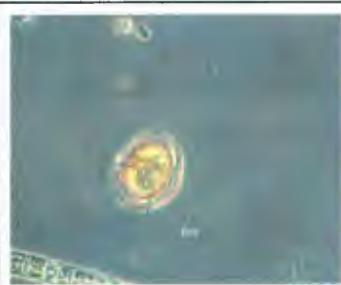
*Nitzschia longissima &
Dinobryon lorica*



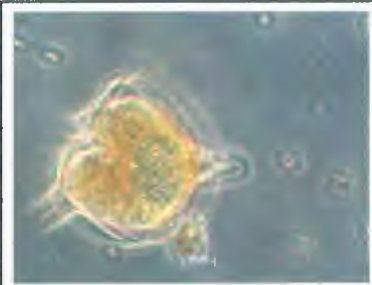
Protoperidinium cf conicum



Protoperidinium curtipes



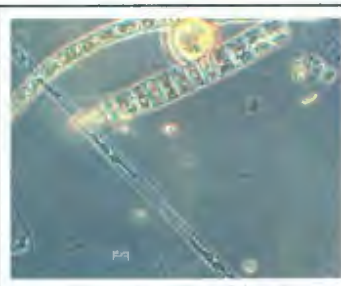
Protoperidinium cf steinii



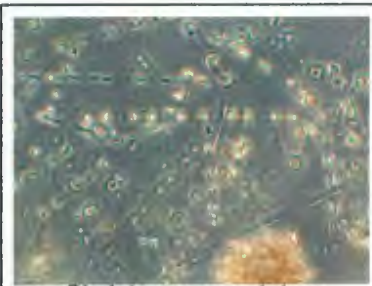
Protoperidinium depressum



*Protoperidinium sp. cf
brevipes*



*Pseudo-nitzschia cf
seriata*



*Skeletonema costatum
(bloom)*



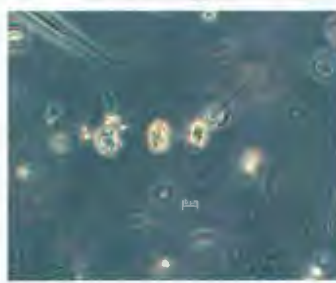
Thalassionema nitzchioides



Thalassiosira anguste-linea



Thalassiosira gravida
(reproducing)



Thalassiosira nordenskioldii

Appendix B

Species counts for ambient and experimental fauna

Table B-1: Species codes

Code	Organism
Aalbtr	<i>Aricidea albatrossae</i>
Acathr	<i>Aricidea cathrinae</i>
Amlind	<i>Ampharete lindstroemi</i>
Aglneo	<i>Aglaophamus neotenus</i>
Ampacu	<i>Ampharete acutifrons</i>
Anolan	<i>Aricidea nolani</i>
Ampdae	<i>Amphaeritidae</i>
Aricsp	<i>Aricidea</i> species
Ampjuv	<i>Amphaeritidae</i> juvenile
Asline	<i>Asebellides lineata</i>
Atetra	<i>Aricidea tetrabranchiata</i>
Capspp	<i>Capitellidae</i> species
Capjuv	<i>Capitellidae</i> juvenile
Chodun	<i>Chone duneri</i>
Chonju	<i>Chone</i> juvenile
Cirdae	<i>Cirritulidae</i>
Clypol	<i>Clymenella polaris</i>
Dorvju	<i>Dorvellidae</i> juvenile
Dorrud	<i>Dorvella rudolphi</i>
Dfimbr	<i>Dorvella</i> Sp.
Etolon	<i>Eteone longa</i>
Etonsp	<i>Eteone</i> species
Etohet	<i>Eteone heteropoda</i>
Eucjuv	<i>Euchone</i> juvenile
Eucpap	<i>Euchone papillosa</i>
Echspp	<i>Euchone</i> species
Eucinc	<i>Euchone incolor</i>
Exodis	<i>Exogone dispar</i>
Faffin	<i>Flabelligera affinis</i>
Glycap	<i>Glycera capitata</i>
Glydae	<i>Glyceridae</i>
Glyjuv	<i>Glyceridae</i> juvenile
Gonjuv	<i>Goniadidae</i> juvenile
Gonmac	<i>Goniada maculata</i>
Gonspp	<i>Goniadidae</i> species
Hmoore	<i>Hartmania moorei</i>
Lumbfr	<i>Lumbrinereis fragilis</i>

Code	Organism
Laonci	<i>Laonice cirrata</i>
Leitfr	<i>Leitoscoloplos fragilis</i>
Lyslov	<i>Lysilla loveni</i>
Maldae	<i>Maldanidae</i>
Medamb	<i>Mediomastus ambiseta</i>
Mthabe	<i>Microphthalmus aberrans</i>
Mthspp	<i>Microphthalmus</i> Sp.
Nepcil	<i>Nephtys ciliata</i>
Nepinc	<i>Nephtys incisa</i>
Niclum	<i>Nicomanche lumbricalis</i>
Oligoc	<i>Oligocheate</i>
Ophacu	<i>Ophelina acuminata</i>
Ophjuv	<i>Ophelidae</i> juvenile
Oprull	<i>Ophelia rullieri</i>
OrbJuv	<i>Orbinidae</i> juvenile
Orbspp	<i>Orbinidae</i> species
Palyra	<i>Paradoneis lyra</i>
Parads	<i>Paradoneis</i> species
Pcirrf	<i>Prionospio cirrifera</i>
Pconch	<i>Polydora concharum</i>
Pecgra	<i>Pectinaria granulata</i>
Pectju	<i>Pectinaria</i> juvenile
Pecspp	<i>Pectinaria</i> species
Pelias	<i>Parougia eliasoni</i>
Pheraf	<i>Pherusa affinis</i>
Phomin	<i>Pholoe minuta</i>
Phtect	<i>Pholoe tecta</i>
Pholju	<i>Pholoe</i> juvenile
Phospp	<i>Pholoe</i> species
Phygro	<i>Phyllodoce groenlandica</i>
Phymac	<i>Phyllodoce maculata</i>
Phymuc	<i>Phyllodoce mucosa</i>
Pister	<i>Pista cristata</i>
Polcau	<i>Polydora caulleryi</i>
Polcir	<i>Polydora ciliata</i>
PolSpp	<i>Polydora</i> species
Praxpr	<i>Praxillella praetermissa</i>

Code	Organism	Code	Organism
Pquadr	<i>Polydora quadrilobata</i>	CrMega	Crab megalope
Psteen	<i>Prionospio steenstrupi</i>	Dialuc	<i>Diastylis lucifera</i>
Pwebst	<i>Polydora websteri</i>	Diapol	<i>Diastylis polita</i>
Pygele	<i>Pygospio elegans</i>	Diaqua	<i>Diastylis quadrispinosa</i>
Rhogra	<i>Rhodine gracilor</i>	Diascu	<i>Diastylis sculpta</i>
Rhospp	<i>Rhodine</i> Sp.	Diassp	<i>Diastylis species</i>
Rhlove	<i>Rhodine loveni</i>	Dulisp	<i>Dulichia</i> Sp.
SabNew	Sabellidae new	Echpar	<i>Echinarachinus parma</i>
Scabde	Scalibregmatidae	Euphau	Euphausiid
Scoarm	<i>Scoloplos armiger</i>	Halira	<i>Halirages</i> Sp.
Sfilic	<i>Spio filicornis</i>	Hipser	<i>Hippomedon serratus</i>
Sjapon	<i>Syllides japonica</i>	Hydroz	Hydrozoan
Slongi	<i>Sphaerosyllis longicaudata</i>	Isopod	Isopod
Spions	<i>Spio species</i>	Isopo1	Isopod 1
Spiosp	<i>Spiophanes species</i>	Isopo2	Isopod 2
Swigly	<i>Spiophanes wigleyi</i>	Lamqua	<i>Lamprops quadriplicatus</i>
Terebe	Terebellidae	Lepamp	<i>Leptostylis ampullacea</i>
ThxSpp	<i>Tharyx species</i>	Metape	<i>Metapella species</i>
UnkPol	Unknown Polychaete	Monspp	<i>Monoculodes</i> Sp.
Astart	<i>Astarte species</i>	Munfab	<i>Munna fabricii</i>
Cerast	<i>Cerastoderma species</i>	Mysids	Mysid
Crenel	<i>Crenella species</i>	Nemert	Nemertean
Macoma	<i>Macoma species</i>	Ophiop	<i>Ophiopholis species</i>
Mytilu	<i>Mytilus species</i>	Phoxce	<i>Phoxocephalus holbilli</i>
Littor	<i>Littorina species</i>	Plepan	<i>Pleustes panoplus</i>
Thyasi	<i>Thyasira species</i>		<i>Strongylocentrotus</i>
Tricho	<i>Trichotropis species</i>	Strdro	<i>droebachiensis</i>
UnIDBv	Unidentified Bivalve	Seaane	Sea anenome
Yoldia	<i>Yoldia species</i>	Sipunc	Sipunculid
AmphiA	Amphipod A	UnkAmp	Unknown Amphipod
AmphiB	Amphipod B	UnkCru	Unknown crustacean
Anthoz	Anthozoan	Unknow	Unknown
Asteri	<i>Asterias species</i>		
Bathym	<i>Bathymedon species</i>		
Caprel	<i>Caprella species</i>		
Chiton	Chiton		
Coroph	<i>Corophium species</i>		

Appendix B-1: Species counts (raw data) for ambient faunal cores (Chapter 1)

Sample	Aalbtr	Acathr	Amlind	Ampdae	Ampjuv	Anolan	Ancsp	Asline	Atetra	Chodun	Chonjv	Dfimbr	Etonsp	Eucjuv	Eucpap	Exodis	Faffin	Glycap	Glyjuv
M8A	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0
M8B	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0
M8C	1	3	0	0	0	1	0	1	2	3	0	0	0	0	0	0	0	0	0
M8D	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
M21A	0	2	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0
M21B	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
M21C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M21D	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
J6A	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
J6B	0	1	0	0	0	1	1	0	1	2	0	0	0	0	0	1	0	0	0
J6C	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
J6D	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	2	1	0	0
J17A	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	0	0
J17B	2	1	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	0
J17C	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0
J17D	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	2	0	0	0
J28A	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
J28B	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
J28C	0	0	0	0	0	1	0	3	2	1	1	0	0	0	0	2	0	0	0
J28D	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0
J123A	1	0	0	1	0	0	0	2	0	0	3	0	0	0	0	6	0	1	1
J123B	0	0	1	3	18	0	0	6	0	0	5	0	0	1	1	1	1	0	0
J123C	1	3	0	0	0	0	0	1	0	2	0	0	0	0	0	2	0	0	0
J123D	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0
A28A	0	0	0	0	2	0	1	3	0	3	0	0	0	0	0	2	0	1	0
A28B	0	0	0	0	0	1	0	3	0	2	0	0	0	0	0	0	0	1	0
A28C	0	0	4	0	0	0	0	7	0	8	0	0	0	0	0	1	0	1	1
A28D	0	0	1	0	0	0	0	4	0	3	0	0	0	0	0	0	0	0	0
S17A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S17B	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1	1	0	0
S17C	0	0	0	0	1	0	0	20	0	4	1	0	0	0	0	5	0	0	0
S17D	1	1	2	0	0	0	0	3	2	3	0	0	0	0	0	2	0	1	0
O14A	1	1	1	0	0	0	1	3	0	3	0	0	0	0	0	0	0	0	0
O14B	0	0	0	0	0	0	0	3	0	2	0	0	0	0	0	3	0	0	0
O14C	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	1	0
O14D	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	2	0	0	0
Totals	8	22	12	4	23	6	4	64	13	69	10	1	1	1	43	3	5	4	1

Appendix B 1 Continued

Sample	Gonjuv	Gonmac	Hmoore	Maldae	Medamb	Mthabe	Mthsp	Nepcil	Nepinc	Oligoc	Ophacu	Oprull	OrbJuv	Palyra	Parads	Pconch	Pecgra	Pectsp	Pelias
M8A	0	0	1	0	0	0	0	1	1	0	1	0	0	0	2	0	0	0	0
M8B	1	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0
M8C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
M8D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
M21A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
M21B	0	0	0	0	0	0	0	0	0	2	0	0	0	0	7	0	0	0	0
M21C	0	0	0	0	0	1	0	0	1	0	0	0	0	0	5	0	3	0	0
M21D	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10	0	0	0	0
J6A	0	0	0	0	0	0	1	1	0	0	0	0	0	0	4	1	0	0	0
J6B	0	1	0	0	1	0	0	0	0	1	0	1	0	0	6	2	1	0	0
J6C	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	1	0	0	0
J6D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	2	0	0
J17A	0	0	0	0	1	0	0	0	0	1	0	4	0	0	4	0	1	0	0
J17B	0	0	0	0	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0
J17C	0	1	0	0	1	0	0	0	0	2	0	0	0	0	6	0	0	0	0
J17D	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	2	0	1
J28A	0	0	0	0	0	0	0	1	0	0	1	0	0	0	3	0	0	0	0
J28B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	1	0	0
J28C	0	1	0	0	0	0	0	0	0	1	0	0	0	0	7	0	1	0	0
J28D	0	0	0	0	0	0	0	0	0	2	2	1	0	0	8	0	0	0	1
J123A	0	0	0	0	1	0	0	0	0	2	0	0	0	0	7	0	0	3	1
J123B	0	0	0	0	0	0	0	0	0	2	1	0	1	0	3	0	1	2	1
J123C	0	0	1	0	1	2	0	1	0	2	2	0	0	0	5	0	0	5	0
J123D	0	0	0	0	1	0	0	0	0	2	0	4	1	0	5	1	2	1	2
A28A	0	0	0	0	1	2	0	0	0	0	0	0	0	0	7	0	0	1	0
A28B	0	1	0	0	1	0	0	0	0	0	0	0	0	0	5	0	0	0	0
A28C	0	1	1	0	0	1	0	0	0	1	0	0	0	0	5	0	0	1	0
A28D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1	0
S17A	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
S17B	0	0	0	0	1	0	0	0	0	1	0	0	0	0	6	0	0	2	0
S17C	0	0	0	0	2	1	0	0	0	0	0	1	0	0	3	1	0	1	0
S17D	0	0	0	1	2	0	0	0	0	0	0	0	0	0	10	0	0	4	0
O14A	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	0	0	2	0
O14B	0	0	0	0	0	3	0	0	0	0	0	0	0	0	12	1	0	0	0
O14C	0	1	0	0	3	0	0	0	0	2	1	0	0	0	3	2	0	1	0
O14D	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0
Totals	1	7	3	1	23	10	2	5	1	23	8	13	2	194	11	14	24	5	1

Appendix B 1 Continued

Sample	Pholjv	Phomin	Phospp	Phtect	Phygro	Phymac	Phymuc	Polcir	Pquadr	Psteen	Pwebst	Pygele	Rhospp	Scoarm	Silic	Sjapon	Slongi	Spions	Swigly
M8A	0	2	0	0	0	0	2	0	0	6	0	0	1	0	0	0	1	0	0
M8B	0	1	0	1	0	0	0	0	0	6	0	0	0	0	1	0	1	0	0
M8C	0	1	0	4	0	0	1	0	0	8	0	0	0	1	0	0	2	0	0
M8D	0	1	0	1	0	0	0	0	0	5	0	0	1	1	0	0	4	0	0
M21A	0	0	0	1	0	1	2	0	0	7	2	0	0	1	0	0	0	0	0
M21B	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1
M21C	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0
M21D	0	3	0	0	0	0	1	0	0	2	0	5	0	0	0	0	1	0	0
J6A	0	0	0	2	0	0	0	0	0	4	0	2	0	0	0	0	1	0	0
J6B	0	1	0	1	0	0	1	0	0	0	1	2	0	0	0	0	1	0	0
J6C	0	0	0	0	0	0	0	0	0	3	0	2	0	1	0	0	0	0	0
J6D	0	0	1	1	0	0	0	0	1	3	0	1	0	1	0	1	0	0	0
J17A	0	0	0	0	0	0	0	0	0	4	0	1	2	0	0	1	2	0	0
J17B	0	5	0	5	0	2	0	0	0	4	0	0	1	0	0	1	5	0	0
J17C	0	0	0	1	0	0	0	0	3	5	1	1	0	0	1	0	0	0	0
J17D	0	2	0	4	0	0	0	0	1	5	0	0	1	0	0	0	0	1	0
J28A	3	2	0	2	0	1	0	0	0	5	0	3	0	0	1	0	2	0	0
J28B	0	2	0	2	1	0	2	0	0	10	1	3	0	0	0	0	0	0	0
J28C	3	1	0	2	0	1	1	0	0	9	0	0	0	0	0	2	2	0	0
J28D	0	0	0	1	0	0	0	0	4	10	0	2	0	1	0	2	1	0	0
J123A	30	1	0	6	0	0	0	0	1	11	1	0	0	0	0	2	2	0	0
J123B	10	0	0	0	0	0	5	0	0	13	0	1	2	0	0	0	0	0	0
J123C	2	2	0	10	0	0	1	0	0	9	0	4	0	4	0	0	3	0	0
J123D	7	0	0	11	0	0	4	0	0	18	0	0	0	0	0	1	0	0	1
A28A	0	1	0	7	0	0	2	1	0	8	0	0	0	0	0	0	1	0	0
A28B	0	0	0	11	0	0	5	0	0	4	0	0	1	1	0	0	1	0	0
A28C	0	1	1	25	0	1	1	0	0	11	0	3	0	3	0	1	1	0	1
A28D	0	1	0	12	0	0	2	0	0	16	0	0	0	3	0	2	0	0	0
S17A	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S17B	0	0	0	5	0	0	0	0	1	2	0	0	2	1	0	0	3	0	0
S17C	0	3	0	13	0	3	2	0	0	17	0	1	1	5	0	0	1	0	0
S17D	0	1	0	20	0	0	1	0	0	9	0	0	0	4	0	0	1	0	0
O14A	0	0	0	20	1	0	1	0	0	11	0	3	0	6	0	0	0	0	0
O14B	0	1	0	17	0	0	0	0	0	4	0	1	0	2	0	1	0	0	0
O14C	0	1	0	7	0	0	5	0	0	4	0	0	0	0	0	0	0	0	0
O14D	0	0	0	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals	55	33	2	204	3	10	39	1	12	233	6	40	12	36	3	14	36	1	3

Appendix B 1 Continued

Sample	ThxSpp	Astart	Cerast	Crenel	Macoma	Mytilu	Thyasa	Tricho	Yoldia	Dialuc	Diaqua	Diascu	Bathym	Monoco	Metape	Phoxce	AmphiA	AmphiB	Caprel
M8A	2	3	3	0	0	0	0	0	0	13	0	0	1	0	0	0	0	0	0
M8B	2	3	3	1	0	0	0	0	0	1	15	0	0	0	0	0	0	0	0
M8C	3	6	2	1	2	2	1	0	1	6	0	1	0	0	0	0	0	0	0
M8D	0	2	3	3	2	0	0	0	0	5	2	4	0	0	0	1	0	0	0
M21A	0	2	0	1	1	0	0	0	0	2	0	0	1	0	0	0	0	0	0
M21B	2	3	2	3	1	0	0	0	0	0	0	0	3	2	0	1	0	0	0
M21C	1	5	0	0	4	1	2	0	0	11	1	2	0	0	0	1	0	0	0
M21D	0	4	2	4	6	0	2	2	0	13	0	0	0	0	0	0	0	0	0
J6A	0	25	2	2	3	0	2	0	0	0	0	2	0	0	0	0	0	0	0
J6B	1	15	2	3	3	0	2	0	1	0	0	1	2	0	0	0	0	0	0
J6C	1	7	5	4	4	0	1	0	0	2	0	3	1	0	0	0	0	0	0
J6D	0	22	3	11	0	0	4	0	0	3	0	0	0	1	0	1	0	0	0
J17A	2	10	1	2	2	0	4	0	0	1	0	0	1	0	0	0	0	0	0
J17B	1	23	1	9	2	5	5	0	0	3	0	1	0	0	1	0	0	0	0
J17C	0	3	2	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
J17D	0	19	1	8	0	1	1	0	0	3	0	0	0	0	0	1	0	0	0
J28A	1	6	0	11	2	0	0	0	0	3	0	0	4	0	0	0	0	0	0
J28B	1	16	1	3	3	0	0	2	0	2	0	0	1	0	0	0	0	0	0
J28C	0	3	2	1	0	0	3	0	0	2	0	1	1	0	0	0	0	0	0
J28D	0	22	0	4	0	0	0	0	0	0	0	0	5	0	0	1	0	0	0
J123A	0	15	0	6	2	0	4	0	0	2	0	0	1	0	0	0	0	0	0
J123B	0	25	1	6	3	1	3	0	1	0	0	0	1	0	1	2	0	0	0
J123C	1	15	0	8	3	1	2	0	0	1	0	0	0	0	0	0	0	0	0
J123D	0	6	0	2	4	2	2	0	1	0	0	0	2	0	0	1	0	0	0
A28A	0	9	2	5	5	0	1	0	0	0	0	8	0	0	0	1	0	0	0
A28B	0	9	5	5	2	0	1	0	0	8	0	0	0	0	1	1	1	0	0
A28C	0	19	1	1	4	0	1	0	0	6	0	2	4	0	1	3	0	0	0
A28D	1	14	15	9	8	0	0	1	0	18	0	8	0	0	0	3	0	0	0
S17A	0	0	0	0	0	0	2	0	0	11	0	0	0	0	0	1	0	0	0
S17B	2	12	6	8	4	0	1	0	0	0	0	0	0	0	2	0	0	0	0
S17C	0	39	15	11	2	0	3	0	0	9	0	0	0	0	1	1	0	0	1
S17D	1	18	7	22	5	0	2	0	0	5	0	0	0	0	1	2	0	1	0
O14A	12	19	7	11	3	0	1	0	0	4	0	5	0	0	0	0	0	0	0
O14B	0	19	9	10	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0
O14C	1	8	1	3	3	0	1	0	0	2	0	1	0	0	0	0	0	0	0
O14D	0	1	6	2	0	0	0	0	0	5	0	1	0	0	0	1	1	0	0
Totals	35	427	110	181	86	13	52	5	5	158	3	41	28	3	8	22	2	1	1

Appendix B 1 Continued

Sample	Strdro	Asten	Isopod	Chiton	Mysids	Ophiop	Nemert	Sipunc	Seaane	Unknow	Totals
M8A	1	1	0	0	0	0	0	0	0	0	48
M8B	1	0	0	0	0	0	0	0	0	0	46
M8C	1	0	0	0	0	0	0	0	0	0	57
M8D	1	0	0	1	0	0	0	0	0	0	44
M21A	0	0	2	0	0	0	0	0	0	0	37
M21B	0	0	0	0	0	0	0	0	0	0	33
M21C	0	0	0	0	0	0	0	0	0	0	43
M21D	2	1	0	0	0	0	0	0	0	0	61
J6A	0	0	0	0	0	0	0	2	0	0	55
J6B	1	0	0	0	0	0	0	1	0	0	59
J6C	0	0	0	0	0	0	2	0	0	0	45
J6D	2	0	0	0	3	0	0	0	0	0	74
J17A	0	0	0	0	0	0	0	1	0	0	51
J17B	2	0	0	0	0	0	0	1	1	0	93
J17C	0	0	0	0	0	0	0	0	0	0	36
J17D	5	1	0	0	0	0	0	1	0	0	72
J28A	2	0	0	0	0	1	0	0	0	0	56
J28B	0	0	0	0	0	0	0	0	0	0	63
J28C	1	1	0	0	0	0	0	0	1	1	58
J28D	1	0	0	0	0	0	0	1	0	0	73
J123A	2	0	0	0	0	0	4	1	0	0	120
J123B	4	0	1	0	0	0	1	1	0	0	129
J123C	1	0	0	0	0	0	0	0	0	0	95
J123D	1	1	0	0	0	0	0	1	0	0	88
A28A	0	0	0	0	0	0	0	0	0	0	74
A28B	1	0	0	0	0	0	0	0	0	0	71
A28C	1	0	0	0	0	0	0	1	0	0	125
A28D	1	0	0	0	0	0	0	0	0	0	128
S17A	0	0	0	0	0	0	0	0	0	0	22
S17B	0	0	0	0	0	0	0	0	0	0	66
S17C	0	0	0	0	0	0	0	1	0	1	170
S17D	1	0	0	0	0	0	0	1	0	0	134
O14A	1	0	0	0	0	0	0	0	0	0	127
O14B	4	0	0	0	0	2	0	1	0	0	99
O14C	0	0	0	0	0	2	0	0	0	0	59
O14D	3	0	0	0	0	0	1	0	0	0	38
Totals	40	5	3	1	3	5	8	14	2	2	2649

Appendix B-2a: Species counts summer experiment chapter 2 diversity/composition experiment

Sample	Aalbtr	Acathr	Agineo	Amlind	Ampdae	Anolan	Asline	Atetra	Capjuv	Chodun	Eucpap	Exodis	Faffin	Glycap	Giyjuv	Gonjuv	Gonmac	Hmoore	Leitfr
1A-1	0	1	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
1B-1	0	3	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0
1C-1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
1D-1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2A-1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
2B-1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2C-1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2D-1	0	1	0	0	0	0	0	1	0	1	2	3	0	0	0	0	0	0	0
3A-1	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
3B-1	2	2	0	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0
3C-1	0	0	0	0	3	1	0	0	0	3	7	0	0	0	0	0	0	0	0
3D-1	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
4A-1	0	10	0	0	1	1	0	0	0	2	1	0	0	0	0	1	0	1	0
4B-1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
4C-1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
4D-1	0	7	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	1	0
5A-1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
5B-1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0
5C-1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
5D-1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
1A-5	0	3	0	0	1	0	3	2	0	1	1	0	0	1	0	0	0	0	0
1B-5	0	2	0	0	0	2	4	0	0	1	1	0	0	0	1	0	0	0	0
1C-5	0	3	0	0	0	0	0	0	2	9	2	0	0	1	0	0	0	0	0
1D-5	0	3	0	0	0	1	2	0	0	2	1	0	0	0	0	0	0	1	0
2A-5	0	0	0	0	0	0	3	0	0	0	3	1	1	1	0	0	0	1	0
2B-5	0	1	0	1	0	0	2	0	0	3	5	0	0	1	0	0	0	0	0
2C-5	0	4	0	1	0	2	4	0	0	0	0	0	1	0	0	0	0	0	0
2D-5	0	0	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
3A-5	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
3B-5	0	2	0	3	0	0	1	0	0	0	3	0	0	0	0	1	1	0	0
3C-5	0	2	0	2	0	2	2	0	0	0	2	2	0	0	0	0	0	0	0
3D-5	0	1	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0
4A-5	1	2	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0
4B-5	0	1	0	0	0	1	2	0	0	0	4	0	0	0	0	0	0	0	0
4C-5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
4D-5	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
5A-5	0	0	0	0	0	0	0	0	0	2	3	0	0	1	0	0	0	0	0
5B-5	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0
5C-5	0	3	0	4	0	0	3	0	0	1	2	0	0	0	1	0	0	1	0
5D-5	0	0	0	2	0	2	8	0	0	0	1	0	2	0	0	0	0	1	0
Totals	6	63	1	20	5	20	41	8	2	30	59	8	6	5	5	2	3	9	1

Appendix B 2a Continued

Sample	Lumbfr	Maldae	Medamb	Mthabe	Mthspp	Nepcil	Nicium	Oligoc	Ophacu	Ophjuv	Oprull	OrbJuv	Palyra	Parads	Pcirrf	Pconch	Pecgra	Pectsp	Pholjv
1A-1	0	0	0	0	0	0	0	1	0	0	0	0	0	10	0	0	0	0	0
1B-1	1	0	0	0	0	0	0	0	1	0	0	0	0	8	0	0	0	0	0
1C-1	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0
1D-1	0	0	0	1	0	0	0	0	0	2	0	0	0	7	1	0	0	0	0
2A-1	0	0	2	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0
2B-1	0	0	0	0	0	0	0	0	1	0	0	0	0	8	1	0	0	1	0
2C-1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
2D-1	0	0	0	2	0	1	0	0	0	0	0	0	0	4	0	1	0	0	0
3A-1	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
3B-1	0	1	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
3C-1	1	0	2	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0
3D-1	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
4A-1	0	0	1	4	0	0	0	0	0	0	1	0	0	11	0	1	0	1	0
4B-1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0
4C-1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
4D-1	0	0	0	4	0	0	0	0	0	0	0	0	0	7	0	0	1	0	0
5A-1	0	0	3	0	0	0	0	0	1	0	0	0	0	10	0	0	0	0	0
5B-1	0	0	3	0	0	0	0	0	0	0	1	0	0	8	0	0	0	0	0
5C-1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0
5D-1	0	0	2	1	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
1A-5	0	0	2	0	0	0	0	0	0	0	0	0	1	12	0	0	0	5	7
1B-5	0	0	0	0	0	0	0	0	0	1	0	0	0	10	0	0	0	1	4
1C-5	0	0	2	2	0	0	0	0	0	0	0	0	0	1	0	0	0	2	2
1D-5	0	0	3	0	0	1	0	0	0	0	1	0	0	5	0	0	0	3	3
2A-5	0	1	4	1	0	1	0	0	0	0	1	0	0	6	0	0	0	8	16
2B-5	0	0	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	2	4
2C-5	0	0	2	0	0	1	0	0	0	0	0	0	0	4	0	0	0	1	6
2D-5	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	0
3A-5	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2
3B-5	0	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0	0	2	8
3C-5	0	0	2	3	1	0	0	1	1	0	1	0	0	7	0	0	0	0	0
3D-5	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	2	5
4A-5	0	0	2	0	0	0	0	0	0	0	0	0	0	8	0	0	0	2	0
4B-5	0	0	2	2	0	0	0	1	0	1	0	0	0	3	0	0	1	5	16
4C-5	0	0	1	1	0	0	0	0	0	0	1	0	0	4	0	0	0	0	2
4D-5	0	0	1	0	0	0	0	1	1	0	0	0	0	2	0	0	0	2	0
5A-5	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	2	2
5B-5	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	16
5C-5	0	0	1	0	0	1	0	0	0	0	1	0	0	3	0	0	0	3	7
5D-5	0	0	1	1	0	0	0	0	0	0	0	0	0	5	0	0	1	0	19
Totals	2	2	45	24	1	6	1	7	7	1	7	1	1	207	3	4	5	43	119

Appendix B 2a Continued

Sample	Phomin	Phtect	Phymac	Phymuc	Polcir	Pquadr	Praxpr	Psteen	Pwebst	Pygele	Rhospp	Scabde	Scoarm	Sfilic	Sjapon	Slongr	Swigly	Terebe	ThxSpp
1A-1	0	3	1	0	0	0	0	7	1	1	0	0	0	0	0	2	0	0	2
1B-1	0	5	0	0	0	0	0	5	2	0	0	0	0	0	0	1	0	0	1
1C-1	0	6	0	1	0	0	0	7	1	0	0	0	0	1	0	0	0	0	0
1D-1	0	0	0	0	0	0	0	19	0	0	0	0	0	1	1	0	1	0	3
2A-1	0	1	0	0	0	1	0	5	1	0	0	0	0	0	0	1	0	0	1
2B-1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3
2C-1	0	2	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
2D-1	1	2	1	1	0	0	0	3	0	3	1	0	0	0	5	2	0	0	0
3A-1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
3B-1	0	0	0	0	0	0	0	8	1	1	0	0	3	0	0	2	0	0	0
3C-1	2	6	0	1	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0
3D-1	1	1	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	1
4A-1	0	1	0	0	0	0	0	11	0	0	0	0	0	0	2	2	0	0	1
4B-1	1	0	0	1	0	0	0	6	0	1	0	0	0	1	1	3	0	0	1
4C-1	1	2	1	0	0	0	0	6	0	0	0	0	0	0	5	4	0	0	0
4D-1	1	1	0	0	0	0	0	5	0	0	0	0	1	0	0	1	0	0	0
5A-1	0	1	0	0	0	1	0	8	0	0	0	0	0	0	1	0	0	0	1
5B-1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	2	1	1	0
5C-1	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	0
5D-1	1	1	0	0	0	0	0	6	0	1	0	0	1	0	1	0	0	0	1
1A-5	0	5	0	1	0	0	0	8	0	0	0	0	0	0	2	0	0	0	0
1B-5	0	2	0	6	0	0	0	6	0	4	0	0	1	0	5	2	0	0	3
1C-5	0	2	0	1	1	1	0	10	0	4	2	1	1	0	0	0	0	0	1
1D-5	0	1	0	2	0	0	0	14	0	0	0	0	0	0	1	1	1	0	4
2A-5	0	3	0	3	0	0	0	12	0	0	0	0	0	0	0	3	1	0	0
2B-5	5	1	1	2	0	0	0	4	0	0	1	0	1	0	0	4	0	0	1
2C-5	0	3	0	1	0	0	0	3	0	0	0	0	1	0	2	3	0	0	3
2D-5	2	0	0	0	0	0	1	13	0	0	0	0	0	1	0	1	0	0	2
3A-5	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	3
3B-5	1	1	0	4	0	1	0	11	0	2	0	0	0	0	1	2	0	0	1
3C-5	0	1	0	3	0	0	0	20	0	1	0	0	0	0	1	0	0	0	0
3D-5	1	2	0	1	0	1	0	11	0	0	0	0	1	0	0	1	1	0	0
4A-5	0	1	2	3	0	1	0	13	0	0	0	0	0	1	0	2	0	0	2
4B-5	1	0	0	2	0	0	0	11	0	3	0	0	0	0	0	0	0	0	0
4C-5	0	0	0	2	0	0	0	12	0	0	0	0	0	0	0	0	0	0	1
4D-5	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	1	1	0	1
5A-5	0	0	0	1	0	0	0	7	0	0	1	0	0	0	2	0	3	0	1
5B-5	1	0	0	1	0	0	0	4	0	0	2	0	1	0	0	5	0	0	0
5C-5	0	0	0	2	0	3	0	12	0	0	2	0	2	0	0	4	0	0	1
5D-5	0	0	0	0	0	1	0	14	0	0	0	0	0	0	3	3	1	0	3
Totals	19	54	7	40	1	12	1	307	7	23	9	1	14	6	34	55	10	1	45

Appendix B 2a Continued

Sample	Astart	Cerast	Crenel	Macoma	Thyas	Tricho	UniDBv	Yoldia	D. lucif	D. polita	Juvum	Bathym	Monoco	Metape	Phoxoco	Caprella	Corophium	S. droe	Asterias
1A-1	8	0	5	3	6	0	0	0	1	1	0	13	1	0	1	0	0	0	0
1B-1	5	1	3	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0
1C-1	1	0	2	1	2	0	0	0	0	0	0	3	1	0	0	0	0	0	1
1D-1	2	2	0	1	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0
2A-1	13	0	4	2	5	0	0	0	1	0	0	2	0	0	0	0	0	1	0
2B-1	7	3	3	1	0	0	0	0	4	0	0	14	2	0	0	0	0	0	0
2C-1	4	0	3	0	0	0	0	0	2	0	0	3	0	0	0	0	0	0	0
2D-1	10	1	9	0	1	0	0	0	3	0	0	2	0	1	1	0	0	0	0
3A-1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0
3B-1	17	1	7	0	0	2	0	0	10	0	0	7	0	0	0	0	0	1	0
3C-1	12	1	12	0	0	0	0	1	4	0	0	3	0	0	0	0	0	0	0
3D-1	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0
4A-1	15	0	1	0	1	0	0	0	4	2	0	7	0	0	0	0	1	0	0
4B-1	4	0	3	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1
4C-1	12	2	6	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
4D-1	7	0	2	3	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
5A-1	5	0	3	1	2	1	0	0	2	0	0	19	0	0	0	0	0	0	0
5B-1	6	0	1	0	3	0	0	0	0	0	0	4	1	0	0	0	0	2	0
5C-1	3	0	1	0	0	0	0	0	2	0	0	9	0	0	0	0	0	0	0
5D-1	2	1	2	0	0	0	0	0	5	0	0	6	1	0	0	0	0	0	0
1A-5	14	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	0
1B-5	0	0	1	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	1
1C-5	7	1	3	0	2	0	1	0	1	0	0	4	0	0	0	0	2	0	1
1D-5	6	0	1	0	1	0	0	0	1	0	0	2	0	0	0	0	3	0	0
2A-5	14	2	7	1	3	0	4	0	6	2	0	1	0	1	0	0	0	0	0
2B-5	5	0	6	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
2C-5	5	1	3	1	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0
2D-5	13	3	8	1	1	0	6	0	12	0	0	2	0	0	0	0	0	1	0
3A-5	1	0	1	0	0	0	0	0	6	1	0	1	0	0	0	0	0	0	0
3B-5	8	1	11	2	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0
3C-5	6	2	6	2	1	1	0	0	1	0	0	1	0	0	0	0	0	2	0
3D-5	2	0	2	0	0	1	0	0	0	0	0	6	0	1	0	0	0	0	0
4A-5	3	0	1	0	0	0	0	0	15	0	0	3	0	0	1	0	0	2	0
4B-5	10	1	2	1	2	0	1	0	0	0	0	1	0	1	0	0	0	0	0
4C-5	6	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4D-5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5A-5	8	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5B-5	3	0	0	2	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0
5C-5	16	1	3	0	0	0	3	0	0	1	136	2	0	0	0	0	0	1	0
5D-5	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals	262	26	124	28	36	5	16	1	89	7	136	139	7	8	3	1	9	15	4

Appendix B 2a Continued

Sample	Ophiop	Hydrozoan	Anthozoan	Isopods	Sipunculid	Nemertean	Unknown	C Totals
1A-1	0	0	0	0	0	1	0	73
1B-1	0	0	0	0	1	0	0	47
1C-1	0	0	0	0	0	0	0	38
1D-1	0	0	0	0	0	0	0	48
2A-1	0	0	0	0	0	0	0	47
2B-1	0	0	0	0	0	0	0	53
2C-1	0	1	0	0	0	0	0	24
2D-1	0	0	0	0	0	1	0	64
3A-1	0	0	0	0	0	0	0	15
3B-1	0	0	0	0	0	0	0	74
3C-1	0	0	0	0	0	0	0	71
3D-1	0	0	0	1	0	0	0	22
4A-1	0	0	0	0	0	0	0	84
4B-1	0	0	0	0	0	0	0	35
4C-1	0	0	0	0	0	0	0	49
4D-1	0	0	0	0	0	0	0	51
5A-1	0	0	0	0	0	0	0	61
5B-1	0	0	1	0	0	0	0	42
5C-1	0	0	0	1	0	0	0	28
5D-1	0	0	0	0	1	0	0	41
1A-5	0	0	0	0	0	0	0	77
1B-5	0	0	0	0	0	0	0	63
1C-5	0	0	0	0	0	0	0	72
1D-5	0	0	0	0	0	0	0	64
2A-5	1	0	0	0	0	0	0	111
2B-5	0	0	0	0	0	0	0	57
2C-5	1	0	0	0	0	0	0	58
2D-5	0	0	0	0	0	0	0	78
3A-5	0	0	0	0	0	0	0	29
3B-5	0	1	0	0	0	0	0	77
3C-5	0	0	0	0	0	1	0	78
3D-5	0	0	0	0	0	0	0	47
4A-5	0	0	0	0	0	1	0	72
4B-5	0	0	2	0	0	1	0	78
4C-5	0	0	0	0	0	0	0	34
4D-5	0	0	0	0	0	0	0	20
5A-5	0	0	0	0	0	0	0	41
5B-5	0	0	0	0	0	1	0	48
5C-5	0	0	0	0	0	0	1	221
5D-5	0	0	0	0	0	1	0	72
Totals	2	2	3	2	2	7	1	2364

Appendix B -2b: Chapter 2 fall experiment diversity/composition

Sample	Aalbtr	Acathr	Agineo	Amlind	Ampdae	Anolan	Anicsp	Asline	Atetra	Chodun	Clypol	Etolon	Etonsp	Eucpap	Echsp	Exodis	Faffin	Glydae	Gonjuv
1A-1	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1	0	0	0
1B-1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	0	0
1C-1	0	0	0	0	0	0	1	1	0	3	0	0	0	2	0	0	1	0	1
1D-1	0	0	0	1	0	0	0	2	1	4	0	0	0	0	0	0	1	0	0
2A-1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2B-1	0	0	0	3	0	0	0	0	2	3	0	0	0	2	0	1	0	0	0
2C-1	0	3	0	0	0	0	0	6	1	5	0	0	0	2	0	0	0	0	0
2D-1	0	0	0	2	0	0	0	8	0	3	0	0	0	2	0	1	0	0	0
3A-1	0	0	0	2	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0
3B-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
3C-1	0	1	0	1	0	0	1	1	0	5	0	0	0	2	0	3	0	0	0
3D-1	0	0	0	0	0	0	0	1	0	3	0	0	0	2	0	0	0	0	0
4A-1	0	2	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0
4B-1	0	0	0	2	0	0	0	6	0	0	0	0	3	3	0	0	1	1	0
4C-1	0	1	0	0	0	0	0	4	0	1	0	0	0	1	0	0	0	0	0
4D-1	0	1	0	0	0	0	0	0	0	4	0	0	0	2	0	0	0	0	0
5A-1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5B-1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
5C-1	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
5D-1	0	0	0	0	0	1	0	5	0	4	0	0	0	1	0	1	0	0	0
1A-5	0	0	0	2	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0
1B-5	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1C-5	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
1D-5	0	0	1	0	0	0	0	3	0	5	0	0	0	1	0	1	2	0	0
2A-5	0	2	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0
2B-5	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2C-5	0	1	0	2	0	0	0	7	0	5	0	1	0	4	0	1	1	0	0
2D-5	0	1	0	1	0	0	0	6	0	3	1	0	0	5	0	2	0	0	0
3A-5	0	1	0	2	0	0	0	2	0	2	0	0	0	0	0	1	0	0	0
3B-5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
3C-5	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
3D-5	0	3	0	1	0	0	0	3	1	3	0	0	0	0	0	0	0	0	0
4A-5	0	3	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
4B-5	0	1	0	1	0	0	0	7	0	2	0	0	0	3	1	0	1	0	0
4C-5	0	2	0	0	0	0	0	3	1	3	0	0	0	3	0	2	0	0	0
4D-5	0	1	0	0	0	2	0	3	0	5	0	0	0	4	0	0	1	0	0
5A-5	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
5B-5	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
5C-5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
5D-5	0	4	0	0	0	0	0	2	0	2	0	1	0	3	0	0	0	0	0
Totals	1	41	2	20	1	5	3	82	8	81	1	2	4	48	1	15	10	1	1

Appendix B-2b: Continued

Sample	Gonmac	Hmoore	Laonci	Lumbfr	Lyslov	Maldae	Medamb	Mthabe	Mthspg	Nepcil	Nepinc	Oligoc	Ophacu	Ophjux	Oprull	OrbJuv	Palyra	Pconch	Pecgra
1A-1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	2	0	0
1B-1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	6	0	0
1C-1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	6	0	0
1D-1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	8	0	0
2A-1	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	0	4	0	0
2B-1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1	0
2C-1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	8	1	1
2D-1	0	1	0	0	0	1	3	0	0	0	0	4	1	0	0	0	3	0	0
3A-1	0	0	0	0	0	0	1	0	0	0	0	2	2	0	1	0	4	0	0
3B-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
3C-1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	5	0	1
3D-1	0	0	0	0	0	0	2	2	3	0	0	0	0	0	0	0	3	0	1
4A-1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	3	0	1
4B-1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	4	0	3
4C-1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
4D-1	1	0	0	0	0	0	4	0	0	0	0	4	4	0	1	0	11	0	1
5A-1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0
5B-1	0	1	0	0	0	0	2	0	0	0	0	1	0	0	0	0	4	0	0
5C-1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	4	0	0
5D-1	0	0	0	0	0	0	4	0	0	0	0	1	1	0	0	0	4	0	1
1A-5	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	9	0	0
1B-5	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	3	0	0
1C-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
1D-5	0	0	0	0	0	0	2	0	0	0	0	0	2	2	0	0	7	0	0
2A-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2B-5	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	3	0	1
2C-5	0	0	0	0	1	0	3	0	0	0	0	3	0	0	0	0	6	0	4
2D-5	0	1	0	0	1	0	2	0	0	0	0	2	0	1	0	0	9	1	3
3A-5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
3B-5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
3C-5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0
3D-5	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	5	0	0
4A-5	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0	3	0	0
4B-5	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	5	0	1
4C-5	0	0	0	0	0	0	5	0	0	0	0	2	0	0	0	0	7	0	0
4D-5	0	0	1	0	0	0	2	1	0	0	0	2	1	0	0	0	4	0	1
5A-5	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	6	0	0
5B-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1
5C-5	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0
5D-5	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	11	0	1
Totals	4	7	1	1	3	2	46	5	5	2	2	37	18	5	4	1	206	3	21

Appendix B-2b: Continued

Sample	Pectsp	Pelias	Pheraf	Pholjv	Phomin	Phtect	Phymac	Phymuc	Pistcr	Pquadr	Psteen	Pwebst	Pygele	Rhogra	Rhlove	Rhospp	SabNew	Scoarm	Sfilic
1A-1	0	1	0	0	0	14	0	1	0	0	3	0	0	0	0	0	0	0	0
1B-1	0	0	0	0	1	9	0	6	0	0	4	0	0	0	0	0	0	1	0
1C-1	1	0	0	0	0	2	0	7	0	0	4	0	0	0	0	0	0	0	0
1D-1	0	0	0	0	1	2	0	2	0	0	4	0	0	0	0	0	0	2	0
2A-1	0	0	0	0	2	7	0	1	0	0	0	0	0	0	0	0	0	0	0
2B-1	0	0	0	0	1	16	0	3	0	0	4	0	0	0	0	0	0	1	0
2C-1	0	0	0	0	2	21	0	4	0	0	6	0	0	0	0	0	0	0	0
2D-1	0	0	0	0	1	7	1	2	0	0	7	0	1	0	0	1	0	1	0
3A-1	0	0	0	0	1	5	0	4	0	0	4	0	0	0	1	0	0	0	0
3B-1	0	0	0	0	0	2	0	3	0	0	3	0	0	0	0	0	0	1	0
3C-1	0	0	0	0	3	8	0	1	0	1	10	1	3	0	2	0	0	2	0
3D-1	0	0	0	0	1	2	0	1	0	0	4	0	0	0	0	0	0	0	0
4A-1	0	0	0	0	1	8	0	0	0	0	4	0	0	0	0	0	0	2	0
4B-1	0	0	0	0	3	1	0	0	0	0	8	0	1	0	1	0	0	1	0
4C-1	0	0	0	0	1	16	0	0	0	0	8	0	3	0	0	2	0	0	0
4D-1	0	0	0	0	0	23	0	1	0	0	9	0	0	0	0	0	0	3	0
5A-1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
5B-1	0	0	0	0	0	7	0	1	0	0	3	0	2	0	0	0	0	1	0
5C-1	0	0	0	1	0	9	0	0	0	0	0	0	3	0	0	0	0	0	0
5D-1	0	0	0	0	4	18	0	2	0	0	7	0	1	0	0	0	0	1	0
1A-5	0	0	0	0	4	12	0	6	0	0	5	0	0	1	0	1	0	2	0
1B-5	0	0	0	0	2	2	0	3	0	0	2	1	0	0	0	0	0	0	0
1C-5	0	0	0	0	0	1	0	2	0	0	2	0	1	0	0	0	0	1	0
1D-5	0	0	0	0	0	15	0	2	0	0	6	0	0	0	0	0	0	1	0
2A-5	0	0	0	0	0	3	0	3	0	0	1	0	0	0	0	0	0	1	0
2B-5	0	0	0	0	2	11	0	0	0	0	0	0	0	0	0	0	0	3	0
2C-5	0	0	0	1	2	12	3	2	0	0	10	0	0	0	0	0	0	0	1
2D-5	0	0	0	0	0	18	2	3	0	0	6	0	2	0	0	0	0	0	0
3A-5	0	0	0	0	0	0	0	4	0	0	2	0	0	0	0	0	0	1	0
3B-5	0	0	0	0	1	7	0	1	0	0	5	0	0	0	0	0	0	2	0
3C-5	0	0	0	0	1	1	1	3	0	0	2	0	0	0	0	2	0	0	0
3D-5	0	0	0	0	1	14	0	3	0	0	9	0	3	0	0	2	0	1	1
4A-5	0	0	0	0	0	3	0	1	0	0	4	0	0	0	0	0	0	0	0
4B-5	0	0	1	0	2	6	0	1	0	0	4	0	0	0	0	1	0	2	0
4C-5	0	0	0	0	2	30	1	1	1	0	8	0	0	0	0	0	1	2	0
4D-5	0	0	0	0	2	16	0	2	0	0	2	0	0	0	0	0	0	2	0
5A-5	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
5B-5	0	0	0	0	1	4	0	1	0	0	3	0	0	0	0	0	0	0	0
5C-5	0	0	0	0	3	10	0	5	0	0	1	0	2	0	0	0	0	0	0
5D-5	0	0	0	0	2	6	0	2	0	0	14	0	1	1	0	0	0	1	0
Totals	1	1	1	3	46	349	8	85	1	1	183	2	23	2	4	9	1	35	2

Appendix B-2b: Continued

Sample	Sjapon	Slongi	SpioSP	Terebe	ThxSpp	Astart	Cerast	Crenel	Littor	Macoma	Mytilu	Thyasi	Tricho	UnIDBv	Yoldia	D lucif	Dsculp	Diassp	AmphiA
1A-1	0	2	0	0	0	7	3	3	0	1	0	0	0	1	0	2	0	0	1
1B-1	0	1	0	0	3	7	0	4	0	1	0	1	0	0	0	0	0	0	0
1C-1	0	0	0	0	2	3	1	2	0	0	1	0	0	0	0	3	0	0	0
1D-1	0	1	0	0	3	11	1	3	0	0	0	2	0	0	0	8	0	0	0
2A-1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	21	0	0	0
2B-1	1	3	0	0	1	6	9	2	0	1	1	0	1	0	0	15	0	0	0
2C-1	0	0	0	0	4	9	3	2	0	0	0	0	0	0	0	9	0	0	0
2D-1	3	0	0	0	4	28	3	26	0	0	0	0	0	0	0	1	0	0	0
3A-1	0	0	0	0	0	3	4	1	1	0	0	0	0	0	0	12	0	1	0
3B-1	0	0	0	0	0	5	3	0	0	0	0	1	0	0	0	2	0	0	0
3C-1	2	0	0	0	1	11	8	13	0	0	0	2	0	1	0	6	0	0	0
3D-1	1	3	0	0	0	6	4	5	0	0	0	3	0	0	0	7	0	0	0
4A-1	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	5	0	0	0
4B-1	1	1	0	0	1	2	14	6	1	1	0	0	0	0	0	2	0	0	0
4C-1	5	1	0	0	4	25	7	13	0	0	1	1	0	0	1	0	0	0	0
4D-1	1	0	0	0	2	4	2	1	0	0	0	3	0	0	0	10	0	0	0
5A-1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0
5B-1	2	0	0	0	0	4	0	0	0	0	0	0	0	0	0	5	1	0	0
5C-1	1	0	0	0	0	7	7	3	0	0	0	0	0	0	0	7	0	0	0
5D-1	1	0	0	0	2	14	11	11	0	0	0	0	0	0	0	11	0	0	0
1A-5	0	0	0	0	1	14	3	6	0	0	0	1	0	0	0	5	0	0	0
1B-5	0	1	0	0	0	2	2	1	0	0	0	2	0	0	0	5	1	0	0
1C-5	0	0	0	0	0	12	1	4	0	0	0	0	0	0	0	7	1	0	0
1D-5	2	0	0	0	2	11	5	4	0	0	1	2	0	0	0	8	1	0	1
2A-5	1	1	0	1	1	6	7	1	0	0	1	2	0	0	0	2	1	0	0
2B-5	0	1	0	0	0	8	5	2	0	0	0	2	0	0	0	5	1	0	0
2C-5	2	3	0	0	7	28	5	26	0	0	0	7	0	0	0	7	1	0	0
2D-5	2	0	0	0	3	34	3	32	0	0	0	0	0	0	0	4	0	0	0
3A-5	0	0	0	0	0	4	0	0	0	0	0	1	0	0	0	4	0	0	0
3B-5	0	1	0	0	3	1	0	3	0	0	0	1	0	0	0	4	0	0	0
3C-5	0	0	0	0	1	7	4	8	0	0	0	0	0	0	0	7	0	0	0
3D-5	1	0	0	0	0	18	1	17	0	3	0	1	0	0	0	6	0	0	0
4A-5	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	2	1	0	0
4B-5	0	2	0	0	1	7	5	6	0	0	0	1	0	0	0	0	0	0	0
4C-5	3	1	1	0	1	20	2	10	0	0	0	1	0	0	0	1	0	0	0
4D-5	3	1	0	0	4	12	4	3	0	0	0	1	0	0	0	1	1	0	0
5A-5	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	5	0	0	0
5B-5	1	1	0	0	1	3	2	2	0	0	0	0	0	0	0	0	0	0	0
5C-5	0	1	0	0	0	8	6	1	0	1	0	1	0	2	0	9	0	0	0
5D-5	1	1	0	0	3	8	2	7	1	0	0	0	0	0	0	4	0	0	0
Totals	34	26	1	1	59	355	147	230	3	8	5	36	1	4	1	215	9	1	2

Appendix B-2b: Continued

Sample	AmphiB	Bathym	Metape	Phoxoce	Corophium	UnkAmp	Euphau	Isopod1	Isopod2	S droe	Asterias	Ophiop	Sipunculid	Nemertear	Echpar	CrMega	Chiton	Littor	Totals
1A-1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	2	0	0	0	54
1B-1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	54
1C-1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	45
1D-1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60
2A-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
2B-1	0	0	0	2	1	0	0	1	0	0	0	1	0	1	0	0	0	0	94
2C-1	0	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	96
2D-1	0	0	0	0	0	1	0	0	0	1	0	1	0	2	0	0	0	0	120
3A-1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	56
3B-1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
3C-1	0	1	0	0	0	0	0	0	0	1	0	3	0	1	0	0	0	0	104
3D-1	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0	0	0	58
4A-1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	41
4B-1	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	74
4C-1	0	3	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	111
4D-1	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	97
5A-1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	17
5B-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36
5C-1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	51
5D-1	0	1	0	0	1	0	0	0	0	1	0	1	2	1	0	0	0	0	113
1A-5	0	0	2	1	0	0	1	0	0	3	1	0	0	0	0	0	0	0	86
1B-5	0	0	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	37
1C-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40
1D-5	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	92
2A-5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	41
2B-5	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	57
2C-5	0	0	3	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	163
2D-5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	151
3A-5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	27
3B-5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40
3C-5	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	48
3D-5	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	102
4A-5	0	0	0	0	0	0	0	0	0	2	1	0	2	0	0	0	0	0	35
4B-5	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	1	69
4C-5	0	0	2	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	120
4D-5	1	0	1	0	0	0	0	0	0	0	0	5	0	1	0	0	0	1	91
5A-5	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	26
5B-5	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	30
5C-5	1	1	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	63
5D-5	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	83
Totals	2	14	12	23	5	2	2	4	6	34	6	19	6	14	1	2	1	3	2751

Appendix B-1a: Chapter 3 summer experiment (quantity)

Sample	Aalbtr	Acathr	Ampacu	Amlind	Ampdae	Anolan	Aricsp	Asline	Atetra	Chodun	Cirdae	Donyv	Dorrud	Etohet	Eucpap	Eucinc	Exodis	Faffin	Glyjuv
1A-1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0
1B-1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1C-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1D-1	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
2A-1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2B-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2C-1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2D-1	1	0	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0
3A-1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
3B-1	2	5	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
3C-1	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0
3D-1	1	1	0	0	0	1	0	0	0	0	3	0	0	0	0	2	0	0	0
1A-5	0	3	0	1	0	1	0	3	0	0	0	0	0	0	0	3	0	0	1
1B-5	0	2	0	0	0	0	0	1	0	2	0	0	0	0	0	2	0	0	0
1C-5	0	3	0	0	0	1	0	4	0	3	0	1	0	0	0	1	0	0	0
1D-5	0	0	0	0	0	0	0	5	0	4	0	0	0	0	0	2	0	0	0
2A-5	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0
2B-5	0	1	0	0	0	0	0	5	1	7	0	0	0	0	1	7	0	4	0
2C-5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2D-5	0	0	0	3	0	2	1	2	0	0	0	0	0	0	0	1	0	0	0
3A-5	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
3B-5	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	3	0	0	1
3C-5	0	3	0	0	0	0	0	7	1	2	0	0	0	0	0	0	0	0	0
3D-5	0	2	0	0	0	0	0	3	0	1	0	0	0	0	0	2	0	0	0
Totals	5	28	1	6	1	12	2	35	5	27	1	2	1	1	1	30	1	4	1

Appendix B-3a Continued

Sample	Gonjuv	Gonmac	Hmoore	Lumbfr	Maldae	Medamb	Mthabe	Mthsp	Nepcil	Oligoc	Ophacu	Ophjuv	Oprull	OrbJuv	Palyra	Pcirrf	Pconch	Pecgra	Pectjv
1A-1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	7	0	0	0	0
1B-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0
1C-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
1D-1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	4	0	0	0	0
2A-1	0	0	0	0	0	1	0	0	0	4	0	0	0	0	10	0	0	0	0
2B-1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	8	0	1	0	2
2C-1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	3	0	0	0	0
2D-1	0	1	0	0	0	0	5	0	0	0	0	0	0	0	1	0	0	0	1
3A-1	0	1	0	0	0	0	2	0	1	0	0	1	3	0	6	0	0	0	0
3B-1	0	0	0	0	0	0	0	0	2	0	0	0	1	0	4	0	0	1	0
3C-1	0	0	0	0	0	1	6	0	0	0	0	0	2	0	0	0	1	0	4
3D-1	1	0	1	0	0	2	1	0	1	0	0	0	0	0	6	1	0	0	0
1A-5	0	0	1	0	0	1	0	0	0	1	0	0	0	0	4	0	0	2	0
1B-5	0	0	0	0	0	2	1	0	0	0	0	0	0	0	7	0	1	1	0
1C-5	0	0	1	0	0	1	0	0	0	0	0	0	0	0	7	0	1	4	0
1D-5	0	0	1	1	0	0	0	0	0	0	0	0	0	0	7	0	1	1	0
2A-5	0	0	1	0	1	1	1	0	0	1	0	0	0	0	9	0	0	1	0
2B-5	0	1	0	0	0	0	0	0	0	1	0	0	2	0	3	0	1	8	0
2C-5	0	0	1	1	0	3	0	0	1	2	0	0	0	0	6	0	0	2	0
2D-5	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
3A-5	0	0	0	0	0	1	0	0	0	0	0	0	0	2	9	0	0	2	0
3B-5	0	0	0	0	0	1	12	0	0	0	2	0	1	0	2	0	0	6	0
3C-5	0	0	1	0	0	1	0	0	0	0	1	0	0	3	5	0	0	4	0
3D-5	0	0	3	0	0	0	0	0	0	0	0	0	0	3	1	0	1	3	0
Totals	1	3	11	2	2	18	30	1	5	12	3	1	10	8	128	1	7	36	7

Appendix B-3a: Continued

Sample	Pholjv	Phomin	Phosp	Phtect	Phymac	Phymuc	Polcau	PolSpp	Pquadr	Psteen	Pwebst	Pygele	Rhogra	Rhlove	Rhospp	Scoarm	Sfilic	Sjapon	Slongi	
1A-1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0	2
1B-1	2	1	0	1	0	1	0	0	1	1	1	4	0	0	0	0	0	0	1	0
1C-1	0	0	0	0	0	1	0	0	2	4	0	0	0	0	0	0	1	0	0	2
1D-1	1	1	0	1	0	0	0	0	1	4	1	0	0	0	0	0	0	1	2	0
2A-1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
2B-1	0	1	0	2	0	1	0	0	0	3	0	1	1	0	0	0	0	0	0	0
2C-1	0	0	0	0	0	0	1	0	1	1	0	4	0	0	0	0	0	0	0	0
2D-1	1	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	1
3A-1	0	1	0	2	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
3B-1	1	2	0	1	0	0	1	0	0	2	2	4	0	3	0	0	0	0	0	0
3C-1	1	2	0	4	0	0	0	0	2	11	0	0	0	0	0	0	1	0	1	0
3D-1	0	1	0	2	0	1	0	0	0	6	0	1	0	0	0	0	1	0	1	1
1A-5	0	2	0	10	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4
1B-5	0	2	0	3	1	1	0	0	0	6	0	8	0	0	0	1	2	0	2	1
1C-5	0	5	0	3	0	2	0	0	0	18	0	0	0	0	0	0	4	0	0	0
1D-5	4	1	0	2	0	2	0	0	0	10	0	0	0	0	0	0	0	0	0	1
2A-5	2	0	0	0	0	3	0	0	0	3	0	4	0	0	0	0	2	0	0	1
2B-5	8	0	0	3	0	0	0	0	1	9	0	0	0	1	0	0	0	0	3	4
2C-5	4	0	0	0	0	3	0	0	0	4	0	0	0	0	0	0	0	0	1	0
2D-5	6	0	0	0	0	3	0	0	0	12	1	0	0	0	0	0	0	0	0	1
3A-5	4	0	0	1	0	3	0	0	0	16	0	0	0	0	0	0	0	0	1	0
3B-5	10	1	2	0	0	1	0	0	1	7	0	10	0	0	0	0	0	0	2	4
3C-5	7	0	0	0	1	0	0	0	1	9	0	1	0	0	0	0	0	0	2	0
3D-5	7	0	0	0	0	2	0	0	0	18	0	0	0	0	0	0	2	0	0	1
Totals	58	21	2	36	2	26	2	1	11	154	5	38	1	5	1	13	3	17	23	

Appendix B-3a: Continued

Sample	Terebe	ThxSpp	UnkPol	Nemert	Astart	Cerast	Crenel	Littor	Macoma	Mytilu	Thyasi	Tricho	UnIDBv	urchin	lepamp	dialuc	diascu	chiton	ophiop
1A-1	0	0	0	0	0	4	2	1	0	2	0	2	0	0	1	0	0	0	0
1B-1	0	0	0	0	0	7	0	2	0	0	0	1	0	0	0	0	0	0	0
1C-1	0	0	0	0	0	6	2	1	0	1	0	1	0	0	1	1	3	0	0
1D-1	0	0	0	0	0	0	5	2	0	0	0	0	0	0	0	0	1	0	3
2A-1	0	2	0	0	0	11	1	1	0	0	1	0	0	0	0	0	1	0	0
2B-1	0	0	0	0	0	13	0	6	1	0	0	0	0	0	0	0	1	0	0
2C-1	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	3	0	0
2D-1	0	3	0	0	0	7	3	7	0	0	0	1	0	0	0	0	2	1	0
3A-1	0	2	0	0	0	12	0	3	0	0	1	2	0	0	0	0	0	0	0
3B-1	0	1	0	0	0	6	2	3	0	1	0	2	1	0	0	0	7	0	0
3C-1	0	4	0	0	0	27	3	14	1	0	2	0	0	0	0	0	3	0	0
3D-1	0	3	0	0	0	4	3	2	0	2	0	1	0	0	0	0	0	0	0
1A-5	0	2	0	0	0	8	0	0	0	0	0	1	0	0	0	0	0	0	0
1B-5	0	1	3	0	0	2	0	2	0	0	1	4	0	0	0	0	0	0	0
1C-5	0	3	0	0	0	2	1	0	1	0	0	0	0	1	0	0	0	1	0
1D-5	1	2	0	0	0	5	3	0	0	0	0	0	0	0	0	0	1	0	0
2A-5	0	1	0	1	0	7	0	3	0	0	0	1	1	0	0	0	2	0	0
2B-5	0	0	0	0	0	10	1	5	2	0	1	2	0	1	3	0	0	0	4
2C-5	0	4	0	0	0	1	1	0	0	0	1	3	0	9	1	0	2	0	0
2D-5	0	3	0	1	0	5	3	7	0	0	1	1	0	3	0	0	1	1	0
3A-5	0	0	0	0	0	4	0	4	0	0	0	1	0	0	1	0	1	0	0
3B-5	0	2	0	0	0	23	1	12	0	3	0	2	0	5	0	0	0	0	0
3C-5	0	1	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0
3D-5	0	2	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
Totals	1	36	3	2		167	31	77	5	9	9	29	2	19	8	1	28	3	3

Appendix B-3a: Continued

Sample	halira	sipunc	plepan	caprel	metape	asteri	cumjuv	seaane	munfab	coroph	monspp	phoxhol	hipser	Totals
1A-1	0	0	0	0	0	0	0	0	0	0	3	2	1	37
1B-1	0	1	0	0	0	0	0	0	0	0	2	0	0	44
1C-1	0	0	0	0	0	0	0	0	0	0	2	0	0	31
1D-1	1	0	0	0	0	0	0	0	0	0	0	0	0	38
2A-1	0	0	0	0	0	0	0	0	0	0	0	0	0	41
2B-1	0	1	0	0	0	0	0	0	0	0	7	0	0	51
2C-1	1	0	0	0	0	0	0	0	0	0	0	0	0	21
2D-1	0	0	1	0	0	0	0	0	0	0	2	0	0	49
3A-1	0	0	0	1	0	0	0	0	0	2	6	1	0	51
3B-1	0	1	0	0	0	0	0	0	0	0	10	0	0	67
3C-1	0	0	0	2	3	0	0	0	0	0	6	0	0	108
3D-1	1	0	0	0	0	0	0	0	0	0	0	0	0	51
1A-5	0	0	0	0	0	0	0	0	0	0	0	0	0	52
1B-5	0	0	0	0	1	0	0	1	0	1	0	0	0	62
1C-5	0	0	0	0	0	1	3	0	0	0	1	0	1	74
1D-5	0	0	0	0	0	0	0	0	0	0	0	0	0	54
2A-5	0	0	0	0	0	0	0	0	0	0	0	0	0	50
2B-5	0	0	0	0	0	1	0	0	1	1	0	1	0	104
2C-5	0	1	0	0	1	0	0	0	0	0	0	0	0	55
2D-5	0	1	0	0	0	0	93	0	0	0	0	0	0	156
3A-5	0	0	0	1	1	0	0	1	1	0	0	0	0	57
3B-5	0	0	0	0	0	0	0	0	0	1	1	0	0	121
3C-5	0	0	0	0	0	0	0	1	0	1	0	0	0	56
3D-5	1	1	0	0	0	0	0	0	0	0	3	0	0	59
Totals	4	6	1	4	6	2	96	3	2	6	43	4	2	1489

Appendix B -3b: Chapter 3 Fall experiment (quantity)

Sample	Acathr	Amlind	Anolan	Ancsp	Asline	Atetra	Capspp	Chodun	Etolon	Eucpap	Exodis	Faffin	Glycap	Gonmac	Gonspp	Hmoore	Lumbfr	Maldae	Medamb
1A-1	2	0	0	1	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0
1B-1	3	0	0	0	0	3	0	0	4	0	0	0	1	0	0	0	0	0	1
1C-1	0	0	0	0	0	9	0	0	3	0	0	0	2	1	1	0	0	0	3
1D-1	0	1	0	0	0	2	0	0	3	0	2	0	0	0	1	0	1	0	1
2A-1	1	1	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	1
2B-1	4	0	2	0	0	0	2	0	0	1	3	1	0	0	0	0	0	0	0
2C-1	1	0	3	0	0	9	2	0	4	0	5	1	0	0	0	0	0	0	1
2D-1	2	0	0	0	0	0	1	0	2	0	0	1	0	0	0	1	0	0	0
3A-1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
3B-1	3	0	1	0	0	2	0	0	7	0	1	0	0	0	0	0	0	0	0
3C-1	1	0	0	0	0	2	1	0	2	1	2	0	1	0	0	0	0	0	0
3D-1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
1A-5	1	0	0	0	0	5	0	0	4	0	0	0	0	0	0	0	0	0	1
1B-5	0	1	1	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	2
1C-5	1	0	0	0	0	5	0	0	2	0	0	0	0	0	0	0	0	0	1
1D-5	0	2	1	0	0	2	0	0	2	0	0	0	0	0	0	0	1	0	4
2A-5	0	0	0	0	0	1	0	0	4	0	2	0	0	0	0	0	0	0	1
2B-5	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1	0	0
2C-5	4	0	0	0	0	0	1	0	3	0	0	0	0	0	1	0	0	0	0
2D-5	1	0	2	0	0	10	1	0	5	0	1	0	1	0	1	0	0	0	2
3A-5	0	1	1	0	0	2	0	0	5	0	2	0	0	0	0	0	0	0	0
3B-5	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	0	1	0	1
3C-5	2	0	0	0	0	1	0	0	4	1	2	0	0	0	1	0	0	0	0
3D-5	1	2	0	1	1	1	0	0	8	0	0	2	0	0	0	0	0	0	2
Totals	29	9	13	1	58	9	1	73	3	28	6	5	5	1	6	1	1	3	21

Appendix B-3b: Continued

Sample	Mthabe	Mthspp	Nepcil	Oligoc	Ophacu	Ophjuv	Oprull	Orbspp	Palyra	Parads	Pconch	Pecgra	Pecspp	Phomin	Phtect	Phymac	Phymuc	PolSpp	Pquadr
1A-1	0	0	0	0	0	2	0	0	0	4	0	0	0	0	0	21	1	0	0
1B-1	0	0	0	0	2	0	0	0	0	8	0	0	1	0	0	7	0	4	1
1C-1	0	0	0	0	0	0	1	0	0	6	0	0	0	0	1	12	0	2	0
1D-1	0	0	0	0	3	0	0	0	0	8	0	0	1	0	1	17	0	1	0
2A-1	0	0	0	0	0	0	2	0	0	3	0	0	0	0	0	9	0	2	0
2B-1	1	0	0	1	1	0	1	0	0	7	0	0	1	0	1	9	0	1	0
2C-1	0	0	0	0	1	0	0	0	0	3	0	0	1	0	0	18	1	2	0
2D-1	1	0	0	0	0	0	0	0	0	7	0	0	1	0	2	14	0	1	0
3A-1	0	0	0	0	0	0	0	0	0	6	0	1	0	0	0	3	0	5	0
3B-1	0	0	0	1	2	0	0	0	0	1	0	0	2	0	0	3	0	6	0
3C-1	0	0	0	2	3	0	0	0	0	5	0	0	1	0	2	16	0	1	0
3D-1	0	0	0	0	0	0	0	0	0	5	0	0	1	0	2	4	0	3	0
1A-5	0	0	0	1	1	1	0	0	0	4	0	0	1	0	0	31	0	5	0
1B-5	0	0	0	0	0	2	0	0	0	5	0	2	0	0	2	9	1	2	0
1C-5	0	0	0	1	2	0	0	0	0	5	0	0	2	0	0	19	0	2	0
1D-5	0	0	0	0	0	0	0	0	0	7	0	0	0	1	0	10	0	1	0
2A-5	0	0	0	0	0	0	0	0	0	4	0	0	1	0	2	12	0	0	0
2B-5	0	0	0	0	1	0	0	0	0	12	0	0	0	0	1	11	1	2	0
2C-5	0	0	1	1	0	0	0	1	7	7	1	0	1	0	0	3	0	3	0
2D-5	3	0	1	1	0	1	0	0	4	0	0	0	0	0	0	24	0	1	0
3A-5	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	11	0	2	0
3B-5	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	3	0	3	0
3C-5	1	1	0	1	0	0	0	0	7	0	0	0	0	0	1	3	0	3	0
3D-5	0	0	0	0	0	0	0	0	3	0	0	1	0	2	3	0	2	0	0
Totals	6	1	2	14	14	4	4	1	126	1	3	15	1	18	272	4	54	1	1

Appendix B-3b: Continued

Sample	Psteen	Pygele	Rhogra	Rhospp	SabNew	Scoarm	Sjapon	Slongi	Terebe	ThxSpp	Astart	Cerast	Crenel	Littor	Macoma	Mytilu	Thyasa	Tricho	UnIDBv
1A-1	3	0	0	0	0	0	1	0	0	0	3	8	1	0	0	1	0	0	0
1B-1	1	0	0	0	0	1	0	0	1	1	12	4	3	0	1	0	0	0	1
1C-1	15	5	1	0	0	0	1	1	0	2	17	8	4	0	1	1	2	0	0
1D-1	3	0	0	0	0	0	2	1	0	2	10	4	5	0	0	1	0	0	1
2A-1	2	0	0	0	0	1	0	1	0	2	3	0	4	0	0	0	3	0	0
2B-1	7	0	0	1	0	3	0	1	0	1	11	1	9	0	0	0	0	0	0
2C-1	23	1	0	0	0	0	0	1	0	1	16	6	14	0	0	1	2	0	0
2D-1	4	0	0	0	0	2	2	3	0	1	16	4	2	0	0	0	0	0	2
3A-1	7	0	0	2	0	0	0	1	0	0	1	4	0	0	0	0	0	0	0
3B-1	6	0	1	0	0	1	0	0	0	0	7	5	2	0	0	0	0	0	0
3C-1	3	0	0	0	0	1	1	2	0	2	12	6	2	0	0	0	2	0	0
3D-1	2	1	0	0	0	5	1	2	0	2	18	4	7	0	0	0	1	0	0
1A-5	6	1	0	0	0	0	0	1	0	0	6	4	4	1	1	0	0	1	0
1B-5	2	0	0	0	0	1	0	0	0	0	12	5	3	0	1	0	3	0	0
1C-5	10	1	0	0	0	3	1	4	0	1	6	7	2	0	1	0	0	0	2
1D-5	3	0	0	0	0	1	0	5	0	0	7	7	5	0	1	0	0	0	0
2A-5	9	0	0	0	0	1	0	0	0	3	6	0	2	1	0	0	4	0	0
2B-5	4	0	0	0	0	0	0	0	0	0	6	7	2	0	1	0	2	0	0
2C-5	9	0	0	0	0	1	0	0	0	0	15	0	3	0	0	0	1	0	0
2D-5	11	0	0	1	0	0	0	1	0	1	15	5	16	0	1	0	3	0	0
3A-5	4	0	0	0	0	0	0	1	0	0	0	3	3	0	0	0	2	0	0
3B-5	5	0	0	0	1	0	0	0	0	0	3	2	2	0	0	0	0	0	0
3C-5	4	0	0	0	0	0	0	1	0	0	3	1	1	0	1	0	0	0	0
3D-5	4	0	0	1	0	2	0	0	0	7	9	1	3	0	0	0	2	0	0
Totals	147	9	2	5	1	23	9	26	1	26	214	96	99	2	9	4	27	1	6

Appendix B-3b: Continued

Sample	urchin	dialuc	diascu	diaspp	lamqua	ophiop	halira	sipunc	metape	asteri	seaeae	munfab	nemert	dulisp	euphau	isopod	hipser	phchol	monspg	plepan	coroph	caprel	Totals
1A-1	1	13	0	2	0	0	2	0	0	1	0	0	0	0	0	0	0	1	2	0	1	0	81
1B-1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	68
1C-1	1	9	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	112
1D-1	0	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	78
2A-1	1	7	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	49
2B-1	0	9	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	82
2C-1	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	126
2D-1	0	8	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	83
3A-1	0	25	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	62
3B-1	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
3C-1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	79
3D-1	0	13	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	78
1A-5	1	8	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	94
1B-5	2	4	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	67
1C-5	0	5	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	1	90
1D-5	0	2	0	0	1	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	66
2A-5	3	8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	65
2B-5	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	59
2C-5	1	6	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	66
2D-5	2	2	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	122
3A-5	0	12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	55
3B-5	0	10	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	44
3C-5	1	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	53
3D-5	1	4	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	0	67
Totals	15	197	3	3	2	8	3	3	10	7	1	2	9	1	1	1	5	12	4	1	5	1	1811



